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THE UNIVERSITY OF ALBERTA

ECOLOGY AND PRIMARY PRODUCTION OF HIGH ARCTIC SEDGE-MOSS MEADOWS, DEVON ISLAND, N.W.T., CANADA

by

© Michael Muc

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

IN

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DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "ECOLOGY AND PRIMARY PRODUCTION OF HIGH ARCTIC SEDGE-MOSS MEADOWS, DEVON ISLAND, N.W.T., CANADA" submitted by Michael Muc in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Plant Ecology.

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DEDICATION

To my parents - Peter and Ann, whose sacrifices, generosity, and understanding helped to make their son's aspirations, his realities.

ABSTRACT

Sedge-moss meadows were the dominant (41%, 1767 ha) Truelove Lowland plant community. They developed along a distinctive increasing moisture gradient ('dry' - wet) and constituted three basic community types: frost-boil, hummocky, and wet sedge-moss meadows. Monocots (primarily sedges) were the predominant community plants and provided the major portion of the plant biomass and cover. Carex stans Drej. was the dominant meadow species and was intensively studied from a number of autecological aspects. The studies reported in this thesis represent 1 - 4 seasons of data.

Frost-boil meadows were only partially (58%) vegetated and possessed prominent but poorly vegetated mineral frost-boils. Hummocky meadows were totally vegetated and had a distinctive hummock/hollow physiography. The more uniform topography and plant cover of the wet meadows developed as a result of the seasonal flooding found in these habitats. Community vascular plant composition, microclimate, soil, and physiographic data were collected in representative meadow stands of each community type and provided the data for inter-community comparisons.

Vascular plant cover ranged from 58 - 86% and community stem densities ranged from 1100 - 2200 stems/m^2. The potential meadow growing season averaged 50 days (45 - 55) and although plant growth began immediately after snowmelt (late June - early July), it did not reach its peak development until early to mid-August. Meadow plants showed a net

positive tiller total leaf increment for only a 20 - 40 day interval over the potential growing season. Growth ceased 2 - 3 weeks before the onset of extended periods of inclement weather. Meadow flowering rates were low (< 10%) and reflected the previous season's growth conditions.

Sedge-moss meadow standing crops and primary production peaked by early to mid-August. Monocots, primarily Carex stans, contributed the major (85 - 95%) portion of the community biomass and primary production. Peak season average total biomass ranged from 821 g/m^2 (frost-boil meadow) to 2316 g/m^2 (hummocky meadow). Of the total biomass, 80 - 90% was of belowground structures. The majority (85%) of the root biomass was concentrated in the upper 20 cm of the soil profile. Of the total root biomass 52% consisted of live root material. Total seasonal productivity averaged 87 g/m^2 (frost-boil meadow) to 174 g/m^2 (wet meadow) and reflected an increasing habitat moisture ('dry' - flooded) gradient. Belowground net primary production was 150% higher than the aboveground production.

Seasonal community chlorophyll and photosynthetic leaf area indices paralled the development of the aboveground biomass. Peak community chlorophyll levels ranged from 162 mg/m^2 (frost-boil meadow) to 283 mg/m^2 (wet meadow) and the corresponding green tissue leaf area indices were 0.31 and 0.38. The hummocky meadow, as a result of its higher (70 - 100%) stem densities had a green leaf area index of 0.63.

Sedge carbohydrate levels ranged from 17 - 24% of the total tiller weight. Tiller carbohydrates exhibited a characteristic early season depletion of belowground reserves in maintaining aboveground growth and a corrsepon-ding late season belowground translocation to compensate for these deficits. Reproductive sedge tillers possessed larger aboveground and corresponding lower belowground carbohydrate levels than did non-reproductive tillers.

Woody plants had the highest (> 5000 cal/g) and monocots the lowest (< 4750 cal/g) energy content of any of the meadow plants. Seasonal energy content of the plants varied by less than 2%. Variation in tissue chemical levels were on the order of 15 - 20%. Forb materials had chemical levels 85% higher than those in comparable monocot and woody plant tissues. Live aboveground tissues on the average maintained chemical levels 120% higher than those in dead and in below-ground structures.

The lowland sedge-moss meadows were the most extensively vegetated and most productive plant communities in the Truelove Lowland. These high arctic meadows are merely lati-tundinal extensions of their low arctic counterparts and when compared to similar low arctic meadow communities their plant biomass and physiological parameters were lower (ca. 50%).

Meadow soil moisture was the most important environmental factor and had a positive affect on both community biomass and production. Meadow plants appeared highly efficient in their utilization and conservation of limited nutrient and energy

resources. An ability to 'internally control' the extent of seasonal growth so as to maintain a consistant growth level from year to year, was another successful adaptive strategy used by the meadow plants. The ability of the meadow plants to accomodate the severity of the high arctic environment was a major contribution to their ecological success and importance in the high arctic ecosystem.

ACKNOWLEDGMENTS

Only a single name appears on this thesis but the credit for its completion must be shared by many. Space does not permit listing all of those to whom this credit belongs but their nameless assistance has always been deeply appreciated.

My sincerest appreciation to my supervisor Dr. L.C. Bliss for his helpful comments and excellent guidance in the course of the research and preparation of this thesis. To the members of my thesis committee - Drs. R.T. Coupland, P.R. Gorham, I. Smith, and D.H. Vitt and Mr. T.W. Peters, who have given so generously of their time and resources, many thanks.

To the participants in the Devon Island I.B.P. Tundra Biome Study, too numerous to mention by name but only too easy to remember, my appreciation for your companionship and helpful comments which provided enjoyment and orientation to the research. A special thanks to my colleague in the field, laboratory, and office - Josef Svoboda, for his friendship and counsel in situations mutually shared.

To my field assistants Ken Orich (1970), Gabor Pal (1971), and Lisa Casselman (1972), a particular note of thanks for making it possible to accomplish so much more than could have been achieved by one pair of hands alone. Grateful appreciation to Mrs. Kveta Svoboda for her care and concern in the analysis of laboratory materials. Last but by no means least, my heart felt thanks to my loving wife Leslee whose help in the field and moral support beyond made the preparation of this thesis a less arduous task than it might have been.

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INTRODUCTION

The High Arctic, encompassing regions north of the 70th parallel, consists of a climatically rigorous and biologically depauperate environment. Although sedge-grass meadows are only a minor (2+%) lanscape component in the Queen Elizabeth Islands (Babb and Bliss 1974) they are a very central component of the high arctic ecosystem by virtue of their importance as muskox and waterfowl habitat. Generaly these 'lush' meadow communities are located within coastal lowlands or in valley basins and their development is dependent on impeded drainage. The extensive plant cover and vigorous plant growth of these communities is a sharp contrast to the vegetative sparseness of the predominating true Polar and Polar Semi-desert landscapes.

The Truelove Lowland on the northeastern coastline (75° 33'N, 84° 40' W) of Devon Island, contains representative plant communities of other high arctic areas and an extensive (41% land surface area) development of sedge-moss meadow communities. As a result of its habitat diversity; its logisitc proximity to Resolute Bay, Cornwallis Island; its local population of muskox and variety of wildlife; its limited size and naturally enclosed area; existance of an established (1960) Arctic Institute of North America base camp; and the corresponding accumulation of scientific background information from previous studies, the Truelove Lowland was chosen as the experimental high arctic study site for the Canadian IBP - Tundra Biome Study.

Geographically comparable (°N) IBP - Tundra Biome Studies were conducted in Greenland (Disko Island), U.S.S.R. (Taimyr),and U.S.A. (Barrow, Alaska) (Heal 1971). This study was the only high arctic ecosystem investigation within the IBP Tundra Biome Program.

Early scientific studies in the Truelove Lowland were primarily geological and meteorological in nature (Cowie 1961, Gill 1963, King 1969, Barr 1971). Subsequent biologically-oriented studies were carried out by Barrett (1972), Hussell (1972), and Teeri (1972).

This study was carried out during late June through late August (growing season) of 1970 - 1972 and during early to mid-August (peak season) in 1973. Its objectives were to:

1. Determine the diversity of the lowland sedge-moss meadow complex and quantitatively characterize the major meadow types.

2. Determine the vascular plant standing crops in the major meadow community types and determine the seasonal increment in both aboveground and belowground production.

3. Correlate aboveground plant growth rates and carbohydrate, nutrient, and chlorophyll content to the net primary production with specific reference to the dominant meadow species Carex stans Drej.

4. Compare the differences in biological parameters within the main sedge-moss meadow community types and to a lesser degree with those reported for raised beach and rock outcrop communities.

The sedge-moss meadow studies complimented and drew upon Courtin and Labine's (1976) meadow meteorological studies as well as Walker and Peters' (1976) meadow soil investigations. In turn, these and other data provided the basis for a modelled synthesis (Whitfield 1976) of a sedge-moss meadow system and its role in the overall lowland ecosystem.

TRUELOVE LOWLAND STUDY AREA

Location and Description

Devon Island, with an area of approximately 54000 km^2, is the second largest island in the Queen Elizabeth Islands group (Fig. 1). Collectively the Queen Elizabeth Islands (75°N) and islands immediately south, constitute the Canadian Arctic Archipelago or true High Arctic. Devon Island is considered to lie within the eastern sector of the Canadian Arctic Archipelago.

Devon Island consists of an eastern highland area of Precambrian shield rock covered with an extensive (15568 km^2) ice cap (Koerner 1966); a west central plateau region of crystalline rocks overlain by sediments; and a northern upland area with similar strata but showing evidence of extensive folding and tilting (Dunbar and Greenaway 1956). The major concentrations of plant and animal life on the island occur within coastal lowlands.

The Truelove Lowland (43 km^2) is one of five consecutive coastal lowlands along the northeastern coast of Devon Island and in total they encompass an area of 274 km^2. The Truelove Lowland is dilineated by a shoreline (24 km) on its north and west sides, by steep granitic cliffs (300 m above sea level) on the south side, and equally steep and high sedimentary cliffs on the east side (Fig. 2).

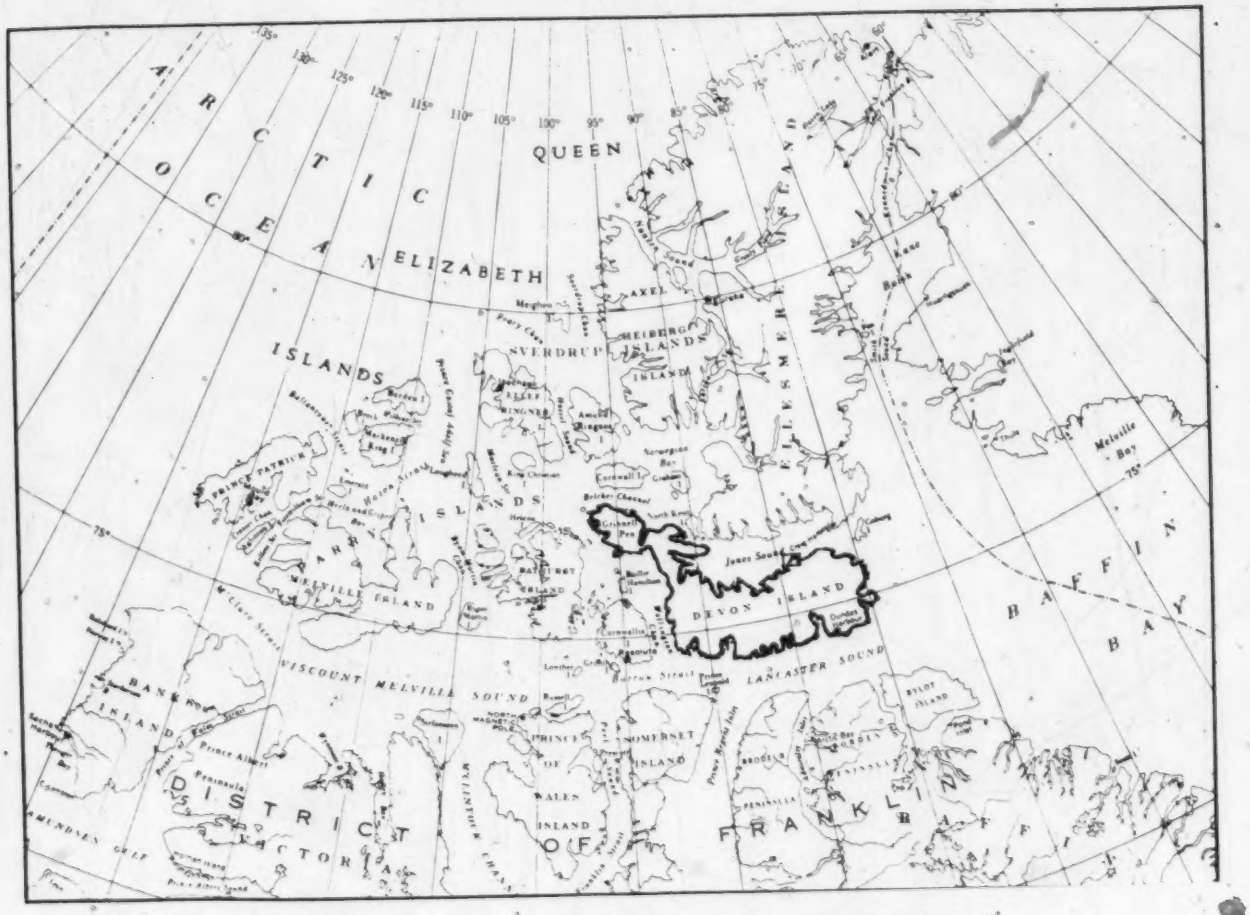

Figure 1. Location of Devon Island and the Truelove Lowland (blocked) study area.

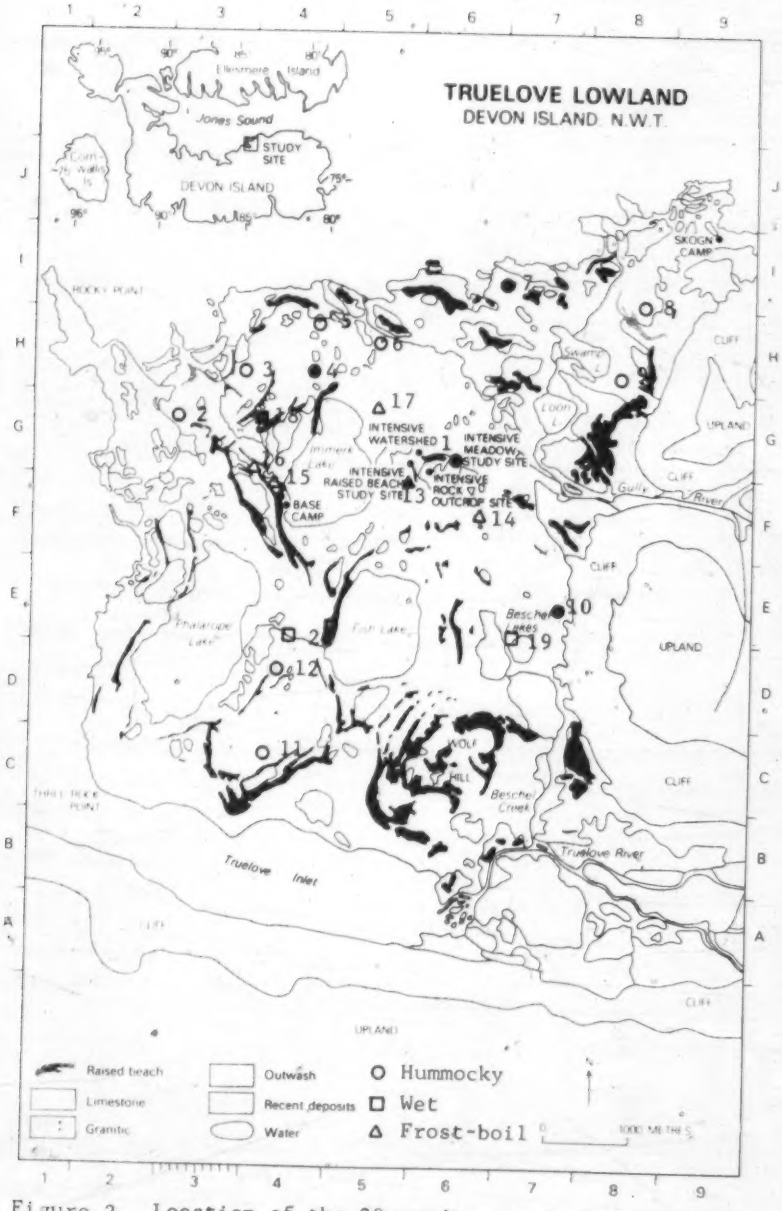

Figure 2. Location of the 20 meadow stands from which production (closed) and/or phytosociological (open) data were collected.

Geology

The basement platform of the Truelove Lowland consists of metamorphic crystalline rocks, primarily granulites and gneisses. The overlying sedimentary deposits consist of a basal deposit of conglomerate sandstone (2-3 m) overlaid by Cambrian dolomitic material. A fault (Tertiary event) along the southern edge of the Truelove Inlet resulted in a subsidence of the northern block by approximately 300 m (Krupicka 1973). Relief in the lowland ranges from 15.2 - 30.5 m (King 1969).

Periglacial History

Radiocarbon datings and ancient lowland marine limits show the area to have been ice-free since ca. 9450 B.P. and the total post-glacial uplift to be on the order of 107 m (Barr 1971). Initial isostatic uplift (2.5 m/century) occurred from 9450 - 8860 B.P.; decreased to 0.9 m/century from 8860 - 7000 B.P.; and has remained at 0.2 m/century over the last 5000 years (King 1969). Recent evidence (Roots 1963) suggests that eustatic rise of the sea may have surpassed isostatic rebound of the lowland by approximately 3.1 m over the last 1000 years. The present day lowland physiography is a reflection of land forming processes active immediately after deglaciation (9450 B.P.) but significantly subdued at the present time (King 1969). Similarily freeze-thaw phenomena such as Solifluction, Cryoturbation, and Congelifraction appear to be less pronounced at the present time.

Physiography

Freshwater bodies cover an extensive portion (ca. 22%) of the lowland area (Table 1). Raised beaches represent 20% of the lowland and granitic rock outcroppings, primarily along the northeastern coastline, another 12%. Radiocarbon datings of lowland raised beaches range from 9360 B.P. along the base of the plateau to 2950 B.P. for a raised beach along the western coastline (Barr 1971). Sedge-moss meadows represent 41% of the lowland area. They primarily develop in poorly drained, low-lying areas between beach ridges. Taking into account the proposed ages of raised beaches in different areas of the lowland and the poor degree of sedge-moss meadow development along the western portion of the lowland, it might be suggested that it takes several thousand years for an area with impounded waters to drain sufficiently for establishment of meadow vegetation. Lowland drainage occurs through three main stream channels (Bliss 1975) which empty into the Truelove River or into Jones Sound. The meadows therefore remain saturated throughout the growing season and are dependent on these moisture conditions to maintain their characteristic vegetation.

Climate

Devon Island is under the influence of a polar climatic regime in which the warmest month's temperatures are greater than 0° C but less than 10° C (Atlas of Canada). Average July and August Truelove Lowland temperatures are $\leq$ 5° C.

Table 1. Major topographic-plant community units (ha, %) within the Truelove Lowland.

Unit	Area (ha)	Lowland (%)
Sedge-moss meadows	1767	41.1
hummocky	884	20.5
frost-boil	795	18.5
wet	88	2.1
Cushion plant-moss (raised beaches)	572	13.3
on raised beaches	274	6.4
separate from raised beaches	233	5.4
with prominent frost-boils	65	1.5
Dwarf shrub heath-moss (rock outcrops)	533	12.4
Cushion plant-lichen (raised beaches)	292	6.8
lowland	215	5.0
rock outcrop	51	1.2
limestone pavement	26	0.6
Lichen barren (limestone pavement)	181	4.2
Lakes and ponds	933	21.7
Salt water marsh	22	0.5
Total	4300	100.0

Although Hare (1970) indicated that the high arctic net annual radiation balance was on the order of 0 - 5 kly, Courtin and Labine (1976) calculated a 1972-1973 Truelove Lowland net annual radiation budget of 17 kly. This is comparable to the net radiation (16 kly) that Hare and Ritchie (1972) reported for Alaska (Low Arctic). The Truelove Lowland would therefore appear to be a climatic anomaly of high arctic regions.

The lowland's unique climate appears to reflect its geographic location on Devon Island. Its proximity to the sea along two perimeters and to steep cliffs along its remaining perimeters may consequently influence its net radiation regime (Courtin and Labine 1976). The extensive (15568 km^2) ice-cap immediately (< 15 km) south of the lowland has been considered (King 1969) an influence on the lowland's climatic regime. This consideration is based on the strong adiabatic winds originating from the ice-cap and and its potential effect on reducing lowland precipitation.

On a geographical comparison, the lowland had similar mean monthly summer (1970-1973) temperatures to those at Resolute, Cornwallis Island (74° N) but lower than those at Eureka, Ellesmere Island (80° N) (Bliss 1975). The annual pattern of net radiation for the Truelove Lowland is one of rapid increase in the early part of June to early July and a subsequent gradual decline until a negative flux is reached in early October. Outside factors (arctic air mass movement and cyclonic activities) vary the degree of

cloudiness and influence the levels of incoming radiation (Courtin and Labine 1976). The effect of cloud cover on incoming radiation is greater in the early part of the summer when the sun's angle is high, than in the latter part of the summer when the sun's angle is low (Courtin and Labine 1976). The net effect is one of annual variability (mid-June to early July) in the time of lowland snow melt. Seasons (1971, 1973) with low cloud cover in late spring, experienced greater incoming radiation levels. This resulted in the time of snowmelt being advanced by up to two weeks over seasons (1970, 1972) in which extensive early-season cloud cover reduced the levels of incoming radiation. Over the project's four year duration (1970 - 1975) summer (June - August) climatic conditions appeared to fit into two distinctive patterns: i) an earlier and milder season (1971, 1973), and ii) a later and cooler season (1970, 1972). A comparative climatic summary of two representative years (1971, 1972) is shown in Table 2. The earlier and milder season was warmer, less windy, and wetter. The majority of July and early August precipitation fell as rain, with snow being common in June and late August. Higher seasonal precipitation rates reflected the occurrance of open lowland lake and ocean (Jones Sound) waters.

Foehn Winds (strong, gusty, dry, and warm) are seasonally infrequent (1 - 3) and tend to occur at the beginning (late June) or end (August) of the growing season. Their biological significance is found in their capacity to cause rapid

Table 2. Mean monthly, seasonal ($\propto$ meadow growing season) Base Camp, Truelove Lowland climatic data for June - August 1971, 1972 and meadow degree days (based on Bliss 1975).

Year		1971			1972		
Environmental Parameter		June	July	August	June	July	August
Radiation ($cal/m^2 \times 10^7$)		20.8	17.2	7.7	19.5	15.8	9.5
Screen Temperature (° C)	Minimum	-2.7	1.0	0.5	-3.9	1.7	1.1
	Mean	-0.3	3.5	2.3	-2.8	2.8	1.8
	Maximum	3.1	5.3	4.7	-1.1	4.4	3.3
Relative air humidity (%)		88	83	79	82	86	87
10 m Wind speed (m/sec)		1.1	2.7	3.7	3.7	3.0	3.3
Precipitation (mm)		0	15.3	34.2	7.6	4.4	9.5
Weeks of T° 0° C			12			7	
Immerk Lake ice free (weeks)			6			0	
Meadow degree days*			443			137	

* accumulated days of air (10 cm) temperatures 0° C.

snowmelt, generally a stressful event for plant and animals in both the early and latter part of the season.

Extensive lowland climatological data (1970 - 1973) have been collected by Courtin from three main intensive sites and four additional extensive sites. These data have in part already been summarized in various IBP progress reports (Courtin 1972, 1973, 1974) and will be fully summarized in the forthcoming project monograph (Courtin and Labine 1976). Computerized and tabulated climatic data are also available at Laurentian University (Department of Biology) and the University of Alberta (Department of Botany).

SEDGE-MOSS MEADOW PERSPECTIVE

The Truelove Lowland has a floristic and faunal composition similar to that of adjacent lowlands - Sverdrup, Sparbo-Hardy, Skogan, and Newman Smith. Although the lowland is climatically atypical of the High Arctic as a whole (Courtin and Labine 1976) it is physiographically comparable to the protected lowlands of the western arctic islands and the protected valleys of Axel Heiberg and Ellesmere Islands (Bliss 1972). From an ecosystem viewpoint only, it is similar to IBP sites at Barrow, Alaska and the Taimyr Peninsula, U.S.S.R., both of which are low arctic regions.

Meadows throughout the High Arctic may be typically characterized as possessing:

1. Saturated soils.
2. Complete bryophyte ground cover.

3. Less extensive vascular plant cover of primarily sedges and grasses.

Meadow topography may range from relatively flat surfaces under extremely wet (flooded) conditions to one of small elevated hummocks amongst low-lying hollow areas in less saturated conditions. Under conditions of shallow soil development and active cryoturbation, unvegetated mineral soil spots (frost-boils) may be found throughout a meadow.

Within the Truelove Lowland sedge-moss meadow complex, three major sedge-moss meadow community types were found:

A. Frost-boil sedge-moss meadows.

B. Hummocky sedge-moss meadows.

C. Wet sedge-moss meadows.

The term community type (a synthetic composite term) is used here to define two or more sedge-moss meadows with similar floristic and physiographic features. Twenty meadow stands (vegetation areas with a uniform floristic and physiographic composition) of these three major community types, were sampled (Fig. 2). These are broken down as follows.

1. Hummocky sedge-moss meadows (stands 1 - 12).

2. Frost-boil sedge-moss meadows (stands 13 - 17).

3. Wet sedge-moss meadows (stands 18 - 20).

The hummocky meadow at site 1 was the project's intensive study meadow site and was intensively studied by most disciplines.

Meadow community data were gathered at each of the meadow stands during the peak (early to mid-August) period of phenological development. Aboveground and belowground standing crop data were collected over various periods of the growing season on a continuous basis for four years (1970 - 1973) at the hummocky intensive study (site 1) meadow and for three consecutive years (1971 - 1973) at the frost-boil (site 13) and wet (site 18) meadows. Only single (1971) season data were collected from three extensive hummocky (sites 4,7,10) meadows.

LOWLAND SEDGE-MOSS MEADOW COMMUNITIES

Within the Canadian Arctic Archipelago (High Arctic) sedge- and grass-dominated meadows are fairly well distributed throughout the islands but on a unit landscape basis account for little (2^{+}%) of the total area of the Queen Elizabeth Islands (Babb and Bliss 1974). They are a more major feature in the landscape of the more southern arctic islands. Arctic plant communities segragate along topographic and moisture gradients (Johnson et al. 1966) with sedge-dominated meadows developing in low-lying, wet habitats. Although these habitats are extremely limited throughout the High Arctic as a whole, in the Truelove Lowland they are a widespread unit and cover 41% (1767 ha) of the total lowland area.

An earlier study of the Truelove Lowland vegetation (Barrett 1972) recognized 9 major plant associations while the IBP project worked on the basis of only seven community

types based on dominant species and growth-form (Bliss 1975). A total of 93 vascular plants had been recorded for the lowland (Barrett and Teeri 1973) and subsequently extended to 94; mosses totalled 135 species; and lichens 260 species (Bliss 1975). The lowland's relatively high vascular plant diversity is proportional to its relatively warm mean summer temperatures. Savile (1972) had previously shown, in a comparison of floral diversity in other high arctic areas, that floristic diversity was more dependent on mean summer temperatures than on latitudinal position.

The meadow classification developed in this study and used throughout the thesis, closely parallels the meadow communities recognized by Barrett (1972) but has the added dimension of complimenting the net primary production studies. The sedge-moss meadow study dealt exclusively with vascular plants. Complimentary bryological studies were done by Vitt and Pakarinen (1976). Lichens were an extremely minor plant component (< 1% cover) and species lists and cover data are found in Barrett's (1972) thesis.

Methods

Quadrat sampling size and frequency for the phyto-sociological analyses in the meadows were derived from calculated species area curves (Greig-Smith 1964). In each of five different lowland meadows, both 50X50 cm and 20X50 cm quadrats were used for vegetation sampling. Both quadrat sizes revealed stability points on their cumulative species area curves with n=10 samples. The rectangular (20X50 cm)

quadrats were selected because of a greater sampling efficiency and the reduction in variance found for this type of quadrat (Cain 1943). Community sampling in stands from which standing crop data were collected had the sample number increased from n=10 (in the strictly phytosociologically sampled stands) to n=16. The six additional quadrats were taken in order to increase the accuracy of plant density counts. The latter counts were to be used in assessing inter-site differences in standing crops and production.

In each meadow stand, the quadrats were distributed in a stratified random pattern. In each quadrat foliar cover (%); individual species vegetative and flowering tiller density; microhabitat (hummock, hollow, frost-boil) cover (%); and thaw depth (cm) were recorded.

Prominence values were calculated for each vascular plant species with a modification of Beals' (1960) formula:

$$PV = \frac{C\sqrt{F}}{10}$$

PV = prominence value
C = cover (%)
F = frequency (%)

Vascular palnt species prominence values only, were used in an agglomerative hierachical (group average) cluster analysis described by Pritchard and Anderson (1971) and modified by P.W. Conway of the Boreal Institute, University of Alberta. The analysis produced a dendrogram of the meadow communities hierarchically linked on the basis of their degree of disimilarity. The inverse relationship (similarity) has been used in this thesis. Prominence values were also used

in Beals' (1960) ordination program revised and extended by M. Easton and D. Prechet of the University of Alberta Computing Services Center.

Nomenclature of the vascular plant species followed that of Porsild (1964). Vascular plant specimens were deposited in the University of Alberta Herbarium (Alberta).

Results

Frost-boil Sedge-moss Meadows

Frost-boil sedge-moss meadows constituted ca. 45% of the total lowland meadow complex. They showed their most extensive development in the central and southern areas of the lowland where extensive fine textured, calcareous alluvial deposits were also found. Characteristically this meadow community type possessed a mosaic surface topography of dense patches of vegetation and poorly vegetated mineral (frost-boil) spots (Fig. 3). Substantial peat accumulations underlay the heavily vegetated areas and and these portions constituted , on the average, 58% of the total meadow surface area. The remaining 42% of the area was covered by the mineral frost-boils. Active (cryoturbation) frost-boils were almost totally devoid of a plant cover and inactive boils possessed a thin (1.5 cm) crust of algal and moss (often Seligeria polaris) material. Vascular plant cover on the frost-boils averaged 10 - 15% and consisted primarily of Eriophorum triste, Carex membranacea, and C. misandra.

The average total meadow vascular plant cover of 58%

Figure 3. A frost-boil (site 13) sedge-moss meadow, featuring prominent sparsely vegetated frost-boils (foreground).

was contributed by 20 species (Table 3). Characteristic species included: Eriophorum triste, Carex membranacea, C. stans, Salix arctica, C. misandra, Arctagrostis latifolia, and Polygonum viviparum. Draba alpina and Braya purpurascens were found exclusively in this meadow type. Two prominent raised beach species - Saxifraga oppositifolia and Dryas integrifolia were also found in the meadows and represented a floristic transition between the meadow and raised beach cushion-plant community. Moss cover averaged 82% and of the 19 species of moss found, dominant ones were: Drepanocladus revolvens, Campylium arcticum, Orthotricum chryseum, Ditrichum flexicaule, Cinclidium arcticum, and Bryum pseudotriquetrum (Pakarinen and Vitt 1973a). Lichen species provided an insignificant (<1%) cover and included Xanthoria elegans, Solorina succata, Mycoblastus sanguianarius (Barrett 1972).

Cluster analysis of the five frost-boil meadow stands (Fig. 4) indicated a minimum community similarity of 55% and a maximum of 75%. The ordination (Fig. 5) identified these meadows as being late in their snowmelt and possessing moist soils.

Hummocky Sedge-moss Meadows

These meadows comprised ca. 50% of the lowland meadow complex. Their distinctive topography consisted of prominent hummocks and hollows (Fig. 6). Hummocks possessed warmer (3 - 5° C) soil temperatures and better aerated and drained soil conditions than were found in hollows. This resulted in

Table 3. Species prominence, plant cover (%), active layer (cm), organic soil cover (%) in five lowland frost-boil sedge-moss meadows.

Stand Number	13	14	15	16	17	Mean
Sampling date	9/8	11/8	16/8	14/8	11/8	
Species	Prominence Value					
Equisetum arvense	2.4	1.8	0.3	0.2	0.6	1.1
E. variegatum	—	0.1	—	0.2	0.1	0.1
Arctagrostis latifolia	3.4	4.1	3.3	16.4	3.4	6.1
Hierochloe pauciflora	0.1	0.1	2.1	3.1	0.1	1.0
Dupontia fisheri	0.4	1.1	0.8	4.1	0.8	1.5
Carex stans	1.9	14.5	23.0	5.4	5.5	10.1
C. atrofusca	0.1					0.1
C. membranacea	29.1	16.5	9.7	11.5	44.8	22.3
C. misandra	6.8	20.9	1.3	3.7	8.4	8.2
Eriophorum triste	18.8	25.0	31.5	20.8	39.0	27.0
Juncus biglumis	2.5	2.1	1.9	0.4	2.8	1.9
Luzula confusa	—	—	0.1	0.1	—	0.1
Salix arctica	6.8	7.4	8.3	15.9	9.7	9.6
Polygonum viviparum	3.4	4.3	2.9	0.6	5.6	3.4
Melandrium apetalum	0.1	—	0.1	0.1	0.1	0.1
Stellaria longipes	—	—	0.1	0.1		0.1
Ranunculus sulphureus	—	—	0.1	0.1	—	0.1
Braya purpurascens	0.1	—	0.1		0.1	0.1
Draba alpina	—	0.1	0.1	0.1	0.1	0.1
Eutremia edwardsii	—	—	0.1	0.3	0.4	0.2
Saxifraga hirculus	—	—	0.6	0.2	0.1	0.2
S. oppositifolia	0.3	2.7	0.1	0.6	3.1	1.4
Dryas integrifolia	0.1	1.1	0.1	0.4	0.1	0.4
Pedicularis sudetica	*	0.6	1.2	0.4	0.1	0.5
P. hirsuta	0.6	*	*	*	*	0.1
Number of species	18	17	22	23	21	20
Vascular plant cover (%)	55	62	63	54	56	58
Moss cover (%)	89	82	82	79	77	82
Open ground (%)	11	18	18	21	23	18
Organic:Mineral soil (%)	51:49	70:30	52:48	67:33	50:50	58:42
Active layer (cm)	56	43	36	59	49	49

* indistinquishable from the other species in the vegetative phase but considered to be less prominent based on lower population flowering levels.

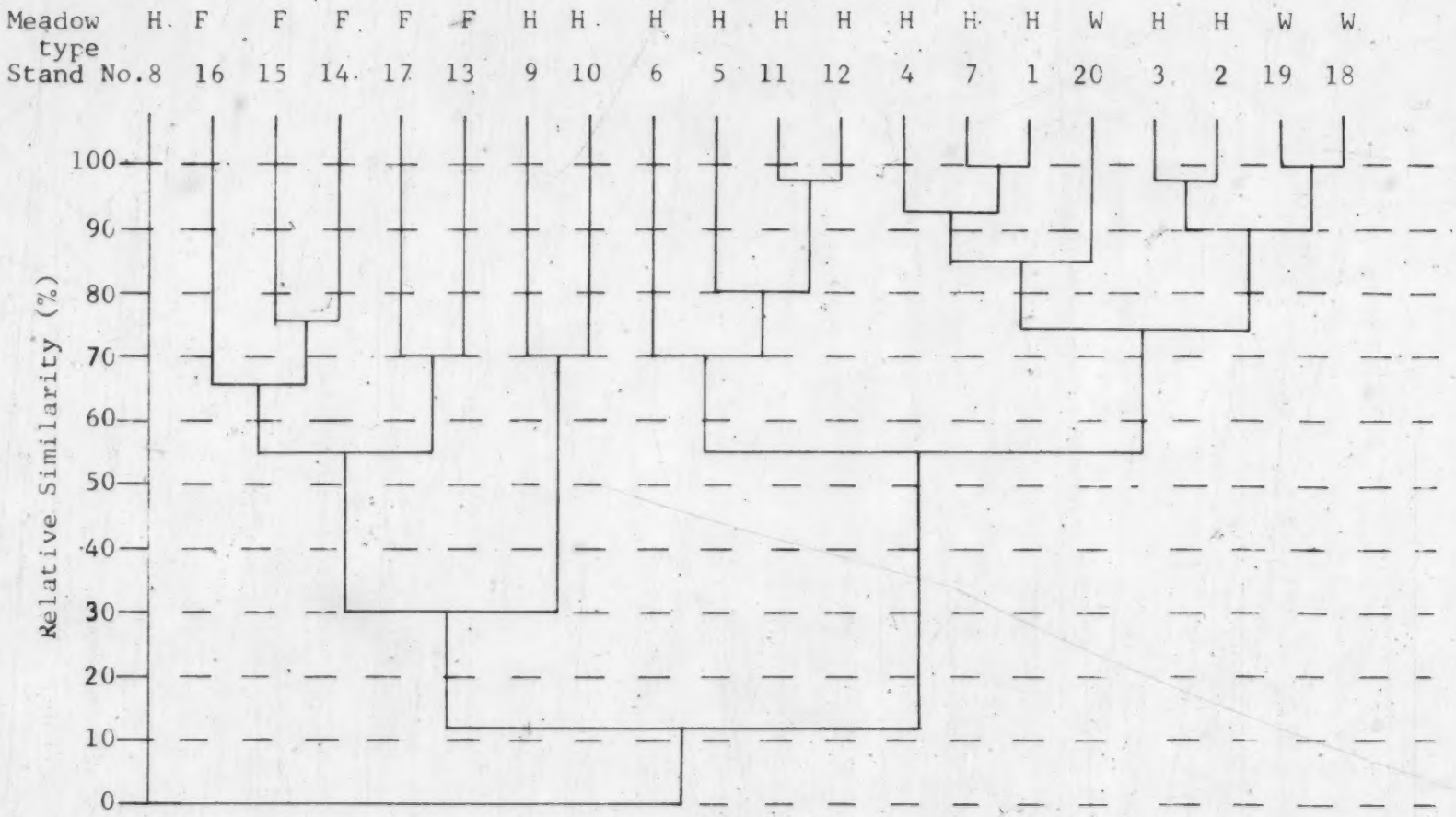

Figure 4. Cluster analysis (group average) based on community species prominence data, of 20 lowland sedge-moss meadow stands (F=frost-boil, H=hummocky, W=wet).

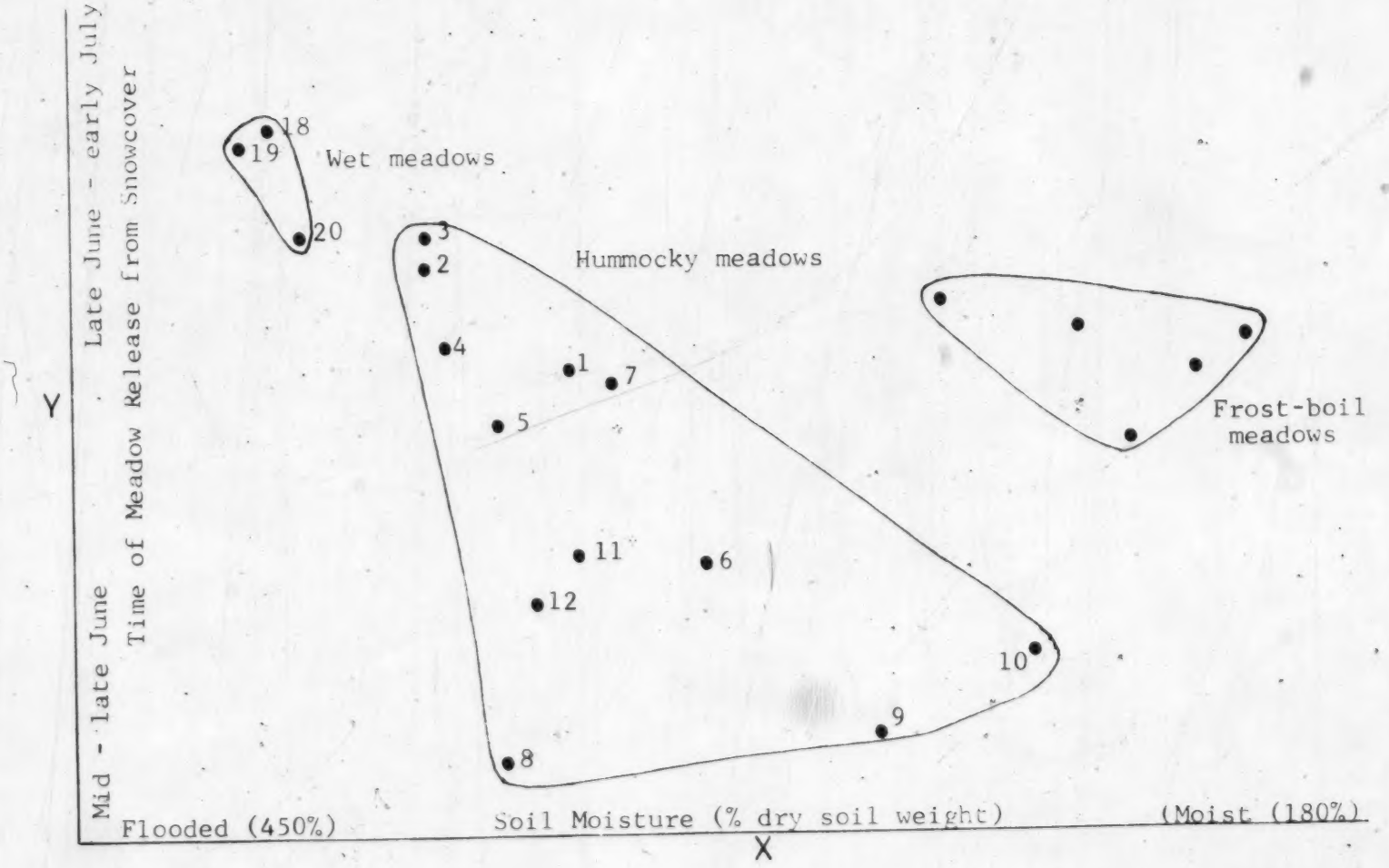

Figure 5. Meadow stand ordination using vascular plant prominence values only, of 20 lowland sedge-moss meadow stands.

Figure 6. A hummocky (site 3) sedge-moss meadow exhibiting a prominent hummock/hollow topography.

a denser woody plant, monocot, and forb growth on hummocks. The colder, flooded hollow habitats had a less dense growth of vascular plants (Fig. 7). Monocots, primarily Carex stans, provided the major hollow vascular plant cover. Bryophytes showed a greater sensitivity to a moisture gradient than did the vascular species and possessed a pronounced hummock and hollow segragation (Pakarinen and Vitt 1973a) Algae also followed a hummock/hollow moisture gradient (Stutz 1976).

Floristically the hummocky meadows averaged 20 vascular species per stand and these provided an average foliar cover of 86% (Table 4). Prominent species included: Carex stans, Eriophorum angustifolium, Salix arctica, C. membranacea, Polygonum viviparum, and Arctagrostis latifolia. Mosses, represented by 30 species, had an average cover of 98% and were dominated by: Drepanocladus revolvens, Cinclidium arcticum, Drepanocladus brevifolius, Campylium arcticum, Orthothecium chryseum, and Riccardia pingius (Pakarinen and Vitt 1973a). Lichen cover was minimal (< 1%) and consisted of Xanthoria elegans, Cladonia pyxidata, and Lecenora epibryon (Barrett 1972).

Cluster analysis (Fig. 4) of the 12 hummocky meadow stands showed that those stands (sites 8,9,10) located along the base of the west-facing plateau were distinctively disimilar from those elsewhere in the lowland. This latter group of hummocky meadow stands had an overall similarity of 55% but also indicated additional stand associations. Well drained coastal meadows (sites 5,6,11,12) were

a.

b.

Figure 7. A hollow (center foreground) and hummock (lower left and right) micro-habitat (a) and a close-up of a hummock (b).

Table 4. Species prominence, plant cover (%), active layer (cm), soil type (organic/gleysolic) and hummock area (%) in 12 lowland hummocky sedge-moss meadows

Stand Number	1	2	3	4	5	6	7	8	9	10	11	12	
Sampling Date	11/8	8/8	8/8	12/8	8/8	9/8	9/8	11/8	9/8	11/8	12/8	12/8	Mean
Species	Prominence Value												
Equisetum arvense	0.2	0.2	0.1	0.1	0.1	0.7	0.3	0.1	1.0	0.2	0.2	0.1	0.3
E. variegatum	—	0.1	—	—	—	—	0.3	—	0.1	0.3	—	—	0.1
Arctagrostis latifolia	1.5	9.5	3.2	2.3	2.3	3.8	0.2	1.7	11.7	13.0	0.1	0.9	4.2
Hierochloe pauciflora	0.3	2.8	1.0	0.9	1.0	0.8	—	0.8	0.2	—	1.0	4.0	1.1
Poa arctica	—	0.2	0.3	—	—	—	—	—	—	—	—	—	0.1
Carex stans	44.0	59.0	63.1	48.0	51.2	39.0	36.3	39.0	15.2	10.2	37.1	33.4	39.6
C. atrofusca	0.4	—	—	—	0.1	—	—	—	—	8.8	1.0	—	0.9
C. membranacea	7.2	0.5	0.1	—	4.2	25.0	12.0	0.5	24.0	14.8	—	1.0	7.4
C. misandra	2.2	—	0.1	0.1	0.1	0.5	0.4	—	0.2	4.1	4.8	2.0	1.2
Eriophorum triste	—	—	—	—	*	*	*	—	—	*	—	—	*
E. angustifolium	11.0	4.7	5.5	8.4	28.0	30.0	9.9	52.0	34.0	24.1	33.6	31.0	22.7
E. scheucherzi	—	—	—	*	—	—	*	*	*	—	—	—	*
Juncus biglumis	0.3	0.8	0.8	0.3	0.8	0.3	1.9	0.2	1.2	4.8	2.6	0.6	1.2
Luzula confusa	1.7	—	—	0.1	0.1	0.2	0.3	0.1	0.2	—	—	0.1	0.2
Salix arctica	7.5	15.2	9.1	11.8	11.7	6.2	8.7	48.0	20.5	15.5	9.8	17.1	11.5
Polygonum viviparum	7.8	3.6	4.3	4.5	5.0	7.5	4.5	7.6	18.0	4.8	4.5	6.4	6.5
Melandrium apetalum	0.1	0.3	0.1	0.1	0.1	0.2	0.1	0.1	0.2	0.1	0.1	0.1	0.1
Stellaria longipes	0.1	0.1	—	0.6	—	0.1	0.1	—	—	—	—	—	0.1
Ranunculus sulphureus	0.1	0.1	—	—	—	—	—	0.1	—	0.1	—	—	0.1
Draba lactea	0.4	0.1	0.1	0.4	0.1	0.2	0.3	0.1	0.1	—	0.1	0.1	0.2
Eutremia edwardsii	0.1	—	—	—	—	—	0.1	—	—	0.1	0.1	—	0.1
Saxifraga cernua	—	0.3	—	0.1	0.2	0.1	0.1	0.6	0.1	—	—	0.1	0.1
S. foliolosa	1.5	0.4	0.2	0.1	0.1	0.1	0.3	0.2	—	—	—	0.1	0.2
S. hirculus	0.7	1.9	0.3	1.4	0.7	0.6	0.6	2.2	0.6	1.5	1.5	2.5	1.2
S. oppositifolia	0.1	—	—	—	—	0.1	—	—	—	—	0.2	0.1	0.1
Dryas integrifolia	0.8	—	—	—	—	—	—	—	—	—	1.5	0.1	0.1
Pedicularis sudetica	1.3	0.5	0.8	0.5	0.5	0.8	0.3	0.5	0.1	0.6	3.8	1.6	0.9
P. hirsuta	*	*	*	*	*	*	*	*	*	*	*	*	*
Number of species	23	20	17	19	20	21	22	19	19	18	18	19	20
Vascular plant cover (%)	90	85	84	88	90	83	85	87	80	78	91	90	86
Moss cover (%)	98	100	100	100	100	98	95	100	100	92	94	96	98
Active layer (cm)	31	22	27	25	26	27	28	29	36	50	27	23	29
Soil (Organic/Gleysolic)	O	G	O	O	G	G	G	G	G	G	O	O	
Hummock area (%)	51	75	56	54	55	68	70	49	75	54	50	70	61

* indistinquishable in the vegetative phase but considered to be less prominent based on its flowering.

distinctive from rock outcrop associated meadows (sites 1, 4,7). Similarily meadows adjacent to late-melting snowbeds (sites 2,3) were recognized as a separate group. The hummocky meadow habitats ranged from those with an early snowmelt and moist soils (site 10) to those with a later snowmelt and saturated (standing water) soils (site 3). On the basis of their ordination, the hummocky meadows appear to be intermediate to the frost-boil and wet meadow community type (Fig. 5).

Wet Sedge-moss Meadows

Meadows of the wet meadow community type have a characteristically uniform topography and a relatively homogeneous monocot plant cover (Fig. 8). These meadows appear restricted, in their development, to inundated pond or stream channel margins and are dependent on the existance of flooded conditions throughout the growing season. Their specialized environmental requirements reduces their coverage to ca. 5% of the lowland meadow complex.

An average wet meadow stand contains 18 vascular plant species and has a vascular plant cover of 77%. Prominent species include: Carex stans, Eriophorum angustifolium, Arctagrostis latifolia, Hierochloe pauciflora, Saxifraga hirculus, and Poa arctica (Table 5). Pleuropogon sabinei, Cardamine pratensis, and Ranunculus hyperboreus are exclusive to these meadows. A total of 17 moss species provided a 100% ground cover. Dominant mosses were: Drepanocladus revolvens, Meesia triquetra, Calliergon giganteum, Cinclidium arcticum,

Figure 8. A wet (site 18) sedge-moss meadow traversed by a permanent stream and exhibiting a characteristic uniform topography.

Table 5. Species prominence, plant cover (%), and active layer (cm) in three lowland wet sedge-moss meadows.

Stand Number	18	19	20	
Sampling Date	9/8	11/8	12/8	Mean
Species	Prominence Value			
Equisetum arvense	—	0.1	—	0.1
E. variegatum	0.1	—	0.1	0.1
Arctagrostis latifolia	6.2	1.0	2.3	3.2
Dupontia fisherii	0.1	0.1	0.5	0.2
Hierochloe pauciflora	0.2	0.4	8.5	3.0
Pleuropogon sabinei	0.1	—	0.1	0.1
Poa arctica	5.0	—	—	1.7
Carex stans	62.3	68.4	46.1	45.6
Eriophorum angustifolium	4.2	4.1	2.9	3.7
E. scheuchzeri	*	*	*	*
Juncus biglumis	0.1	0.1	0.1	0.1
Salix arctica	0.6	0.1	—	0.2
Stellaria longipes	1.0	0.3	0.1	0.5
Ranunculus hyperboreus	0.7	0.1	1.0	0.6
Cardamine pratensis	0.7	0.5	0.1	0.4
Draba lactea	—	0.1	—	0.1
Saxifraga cernua	1.7	0.2	0.2	0.7
S. foliolosa	0.2	0.2	0.1	0.2
S. hirculus	2.5	2.6	1.1	2.1
Pedicularis sudetica	0.1	0.1	0.1	0.1
P. hirsuta	*	*	*	*
Number of species	19	18	17	18
Vascular plant cover (%)	76	80	74	77
Moss cover (%)	100	100	100	100
Active layer (cm)	29	30	33	31

and Drepanocladus brevifolius (Pakarinen and Vitt 1973a). Lichens were entirely absent due to the flooded nature of the meadow habitat.

Cluster analysis (Fig. 4) of the wet meadows showed their inter-site similarity to be 75%. On the ordination (Fig. 5) these meadows were shown to be late in their snowmelt and possessing flooded conditions.

Discussion

Meadows are a relatively restrictive lowland plant habitat and only one-third (34 species) of all the lowland vascular species were to be found growing in the meadows. Successful species were: i) tolerant of cold soils; ii) tolerant of saturated (poorly aerated) soils; and iii) relied on a vegetative mode of reproduction. Carex stans best fits these criteria and consequently was the most abundant and successful meadow species. A low community species diversity and dominance by a few species greatly reduced inter-specific competition but undoubtedly contributed to intra-specific competition. Effects of competition were not examined but would have been most pronounced on the hummock microhabitats.

In both the vascular and bryophyte species abundance, the gradient extended from one of high diversity in the hummocky meadows to one of low diversity in the wet meadows. This gradient corresponded to the more diverse nature of the mesic conditions found in the hummocky meadows and the restrictive nature of the flooded wet meadow habitat.

The overall similarity in vascular species composition of all three meadow community types was an indication of the broad ecological range of most meadow species. Lowland meadow habitats were basically similar and differed primarily in their soil moisture content and soil composition.

Carex stans Drej. is the most productive and abundant of all meadow species. Its wide ecological range (moist tundra to shallow water) allow it to successfully occupy any type of meadow habitat (Wiggins and Thomas 1962). Carex stans was originally regarded as a subspecies of Carex aquatilis (Polunin 1959) but has subsequently been recognised (Porsild 1964) as a valid species. Hulten (1967) showed it to possess a chromosome number different than that of Carex aquatilis.

Carex membranacea and C. misandra favor less saturated soil conditions and are most prominent on hummocks in the hummocky and frost-boil meadows. Eriophorum species also show a distinctive habitat preference. Eriophorum angustifolium and E. scheuchzeri were associated with wet, organic soils and E. triste was associated with moist, calcareous soils such as those found in the frost-boil meadows. The restricted growth of Pleuropogon sabenei and Ranunculus hyperboreus in wet meadows was consistant with their classifcation (Porsild 1964) as obligate freshwater species. Although the meadow habitats were not sufficiently different to become exclusive for the majority of meadow species, habitat preferences were apparent from inter-community comparisons of species

prominence values. Johnson and Packer (1965) have reported similar species/habitat relationships from low arctic communities.

Frost-boil Sedge-moss Meadows

The frost-boil meadows had only slightly more than one-half of their total surface area suitable for plant growth and these areas were characteristically well vegetated. Intensive activity (cryoturbation) within frost-boils of 'youthful' frost-boil meadows severely restricted plant establishment by interfering with rooting. Raup (1971) found that root damage in such habitats were extensive. Vegetation establishment (early stages?) in less active frost-boils resulted in an average cover of 10 - 15%. Eriophorum triste is one of the first species to become established on frost-boils and its usccess may be largely due to its capacity for annual root replacement (Shaver and Billings 1975) and its preference for calcareous soils (Porsild 1964). In the low arctic meadows, Raup (1971) found initial frost-boil vegetation cover to be 2% and Derviz-Sokolova (1966) reported it to be 10% in Russian low arctic meadows. The higher vegetation cover of lowland frost-boils might indicate a more advanced stage of plant invasion.

The vegetated areas of the frost-boil meadows possess a hummock/hollow topography comparable in appearence and area coverage to those of hummocky meadows. Seasonal above-ground production in these areas were 65% of those for

hummocky meadows and their belowground biomass was 30% of the belowground biomass found in the hummocky meadows. The frost-boil meadows constituted the wet portion of the vegetation continuum extending from the moist beach ridge transition zone. A corresponding aboveground plant production gradient can also be shown for this continuum (Svoboda 1974). Barrett (1972) described the frost-boil meadows as the Eriophoro-Salico-Arctagrostidetum association.

Frost-boil meadows appear to be a widespread type of arctic meadow. In North America they have been identified, in low arctic locations, as dry mesic meadows (Holowaychuk et al. 1966), patterned ground communities (Porsild 1955), and ecotonal frost-scar communities (Johnson et al. 1966). In Eurasia comparable communities have been described as spotty shrub sedge-moss (Pavlova 1969), dryad-sedge-moss spotted (Khodachek 1969) and spotted medallion (Aleksandrova 1970a) tundra.

Hummocky Sedge-moss Meadows

The hummocky meadows represented to most favorable and diverse lowland meadow habitat. They possessed higher (900 - 1100 stems/m^2) stem densities and greater aboveground (40 - 65%) and belowground (50 - 210%) biomass than either of the other two meadow types. Microhabitat diversity which ranged from warm and moist conditions in hummocks to cold and wet conditions in hollows, facilitated a wide species diversity. The hummocks thawed earlier and deeper (5 cm) than the hollows and proved to be an optimal habitat for forbs and woody

plants. Similar hummock/plant associations have been described from low arctic meadows (Porsild 1955, Raup 1965, 1969, Beschel and Matveyeva 1972).

The variability in the habitat and floristic prominence of hummocky meadows was associated with their: i) lowland location; ii) environmental conditions (temperature, soil, moisture); and iii) developmental age. Based on periglacial evidence, the coastal hummocky meadows were of more recent origin than those farther inland. Proximity to the ocean also created a colder meadow environment. Meadows within or adjacent to granitic rock outcrops possessed the most optimal habitats. Reradiation from the rocks (heat-sinks) created warmer environmental conditions and meltwaters from snow accumulation in the rock outcrops provided sufficient moisture for plant growth. The plateau-base hummocky meadows were similar, in their floristics and soil conditions, to the frost-boil meadows.

Barrett (1972) described meadows of this type as belonging to the Caricetum stantis association subassociation caricetosum membranacei. Hummocky meadows are also a widespread meadow type in the Low Arctic. Polunin (1948) described similar communities around Dundas Harbor (Devon Island) as grassy sedge communities. On Somerset and Northern Ellesmere Islands similar meadows have been described by Savile (1959, 1964). I have also observed hummocky meadows on Prince of Wales Island and on the Boothia Peninsula. In Eurasia, comparable meadows are identified as hummocky

patterned ground (Aleksandrova 1961) and tussocky sedge-cottongrass low hummock tundra (Filin and Yurtsev 1966). An outstanding latitudinal difference in the vegetation of this meadow type, is the pronounced dominance of Carex sp. in the high arctic meadows and of Eriophorum sp. in the low arctic meadows.

Wet Sedge-moss Meadows

Wet meadows are an extremely specialized community type. Minimal intra-site habitat variability has reduced their species variability and resulted in a relatively uniform vascular plant cover. The almost monospecific (Carex stans) composition of their biomass has resulted in their being the most productive lowland community.

Barrett (1972) placed meadows of this type in the Caricetum stantis association subassociation caricetosum stantis. Elsewhere in the arctic, meadows of this type also possess a limited distribution (Savile 1961). Polunin (1948) described similar meadows around Dundas Harbor (Devon Island) as wet marshes. Beschel (1970) described these high arctic meadows as characteristically being pure stands of Carex stans and reported them found on Axel Heiberg and Ellesmere Islands. In Eurasia, comparable meadows have been described as sedge-hypnum bogs (Filin and Yurtsev 1966), cottongrass sedge tundra (Tikhomirov 1959), and swamp meadows (Gorchakovsky and Andrejashkina 1972).

Lowland Sedge-moss Meadow Perspective

A distinctive overall distribution was observed in the

lowland meadows (Fig. 9). Frost-boil meadows were primarily concentrated in the central (older?) areas of the lowland. These regions were of a depressional nature (lake basin origin?) and underlain by fine alluvial deposits. The overall pattern of their deposition suggested their origin as being from the eastern plateau. Frost-boil meadows were also located on the alluvial slopes along the north side of the Truelove Inlet. Hummocky meadows possessed a more peripheral lowland distribution. They were often found within or adjacent to granitic rock outcrops or in association with beach ridge formations. Wet meadows were irregular in their distribution and limited to areas of seasonal flooding (stream channels, pond margins). Meadow development in the northwestern section of the lowland was limited and sporadic in its occurrence. These areas were considered to be the mostly recently emerged portions of the lowland and as yet had not created conditions suitable for meadow development.

Successional concepts as defined for temperate regions are not applicable, in their entirety, to tundra communities (Churchill and Hanson 1958). The high degree (70%) of species similarity in the lowland sedge-moss meadows could, however, provide the potential for phasic and cyclic changes in species prominence within meadow communities. This could help explain the variable degrees of similarity found, by cluster analysis, in the lowland meadows. The meadow community gradient followed a moisture index, from moist conditions in the frost-boil meadows to flooded conditions

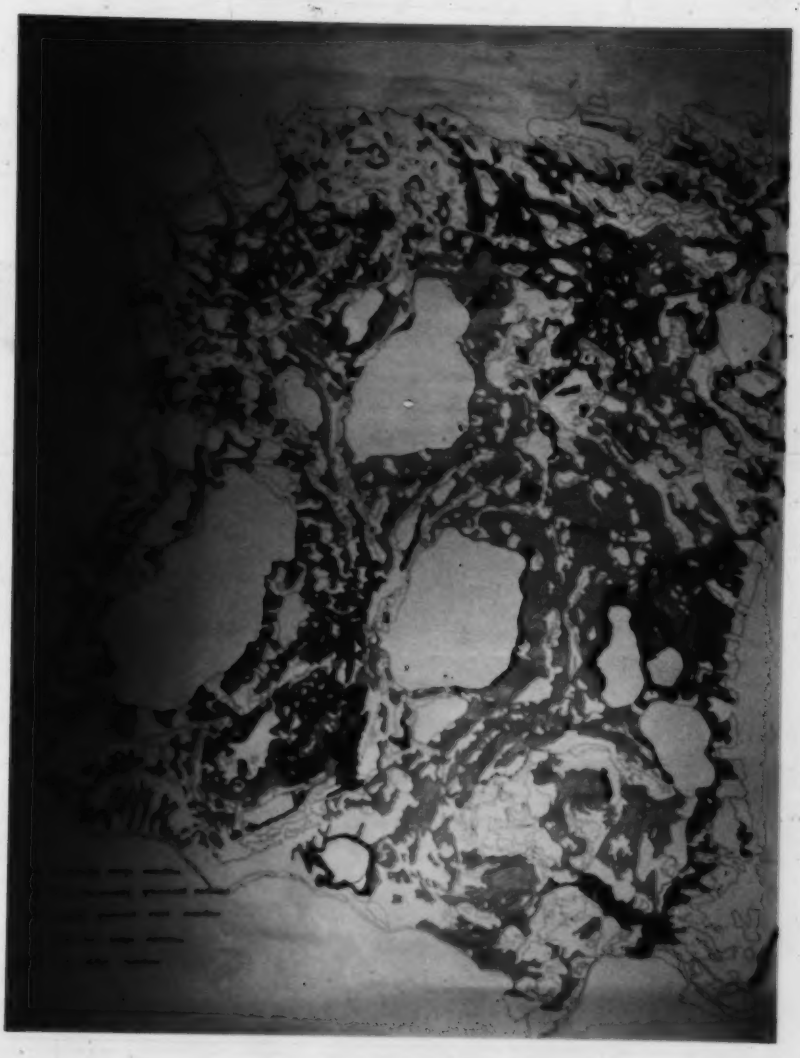

Figure 9. Truelove Lowland map of topographic-plant community units.

in the wet meadows. If community energy conservation and efficiency could be achieved through community stability, then conceivably the frost-boil meadows could develop into hummocky meadows. This pattern of development might help explain the floristic similarity of the plateau-base hummocky meadows (sites 8,9,10) to the frost-boil meadows.

Raup (1965) and Tikhomirov (1966) viewed meadows of the frost-boil type as degraded forms of more mesic (hummocky?) communities. This would not be the case in the Truelove Lowland, where the frost-boil meadows were concentrated in the older portions of the lowland and would therefore be considered to be the oldest meadow type. It was also observed that inactive frost-boil meadows in the process of being totally vegetated, had a surprising resemblance to hummocky meadows. Lowland frost-boil meadows were therefore considered to be of separate origin but to possess the potential for developing into the hummocky type of meadow community.

Wet meadows were closely associated with hummocky meadow communities but a distinctive relationship between the two was more difficult to define. Sigafoos (1951) had suggested that drainage of tundra marsh (wet meadow?) communities would permit the invasion of more mesic species and create a different community (hummocky?). Conversely, it might be suggested that flooding a meadow community would favor the establishment of a community (wet meadow?) of aquatic species. Lowland wet meadows might simply be modified (degraded?) hummocky meadow communities.

MEADOW MICROCLIMATE

Snow cover, vascular plant canopy and upper soil profile temperatures, thaw depth, soil moisture content, and incoming radiation levels are important factors in the development and maintenance of arctic sedge-moss meadows. Diversity in meadow physiography, species composition, plant cover, and primary production are the major manifestations of environmental influences. The extensive (41%) surface area cover and lushness of the lowland meadows indicates an optimal plant growth habitat.

Methods

Snow

Snow depth and density measurements were collected at a hummocky (site 1) and wet (site 18) meadow during June of 1971 and 1972. A single measurement was taken at both sites in May 13, 1972. A frost-boil (site 13) meadow was sampled on only two dates (June 9, 18) in 1971. Depth measurements (n=5) were taken at five permanent snow stations at irregular (ca. 3-day) intervals until total snowmelt. A calibrated (1 cm) steel rod was used. On each sampling date snow density measurements were also taken at each station. A Cold Regions Research and Engineering Laboratory snow-kit (Test Lab. Inc. Chicago) was used.

Active Layer

Seasonal development of the meadow active (thaw) layer was measured at the hummocky (site 1) meadow in 1970 by taking three depth measurements in each plot (n=16) sampled

for production, over the five seasonal harvest dates. In 1971, thaw depth measurements were also taken at a frost-boil (site 13) and wet (site 18) meadow, in conjunction with weekly soil moisture sampling (n=10). Similar data at three additional hummocky (sites 4,7,10) meadows was collected in conjunction with production harvests and involved taking 18 measurements in each sampling period. In 1972, measurements (n=40) were taken only at the three (sites 1,13,18) major meadows. A permanent 10-meter transect was used, with measurements taken at three-day intervals. The 1973 active layer depth was measured (n=25) on a single date (August 5) which approximated the period of maximum thaw in previous years. A calibrated (1 cm) steel rod was used for thaw depth measurements.

Temperature

Detailed temperature data were available for the hummocky intensive study (site 1) meadow from Courtin's permanent meteorological station. Five-day means of these data have been computer tabulated and were used in this thesis. Short-term, less extensive, weekly hygrothermograph data were also available for a wet (site 18), coastal (site 7), and plateau-base (site 10) meadow.

Meadow Greenhouse Microclimate

The potential effects of increased air, soil, and leaf temperatures on arctic meadow plant growth and phenology, were tested (1972) by means of two meadow field greenhouses. An added environmental modification created by the green-

houses was a total reduction in wind effect and creation of supersaturated (Relative Humidity > 100%) air conditions.

Each greenhouse consisted of a 150 X 120 cm framed shelter which was covered with heavy sheet plastic and secured to the ground with tent pegs (Fig. 10). The plastic canopy was kept approximately 15 cm above the plant canopy by means of stakes.

Temperature regimes (5, -1, and -10 cm) within one greenhouse and its adjacent hummock and hollow habitats (controls), were taken with thermocouples (0.125 mm diameter copper-constantan wire).Greenhouse and outside Carex stans leaf (single) temperatures were measured with a 0.003 mil copper constantan clip-on thermocouple. Spot readings were taken, at irregular (ca. three day) intervals between 1100 - 1700 hrs, with a Wescor MJ55 microvoltmeter. On August 15 - 16, continuous hourly measurements were taken for a 24 hr interval.

Results

Snow

Early June (1971) snow depths ranged from 46 - 52 cm in the three meadows and the average snow depth was 39 cm in 1972. Late season snowmelt in 1971 progressed in a linear fashion until total melt occurred on June 25. The corresponding 1972 melt pattern showed only a slight melt rate prior to a sharp increase the week before total melt occurred (July 4) (Fig. 11). No appreciable snow depth increment was found between the May 13 and June 16 (1972)

Figure 10. Meadow field greenhouse and adjacent thermocouple station (left foreground).

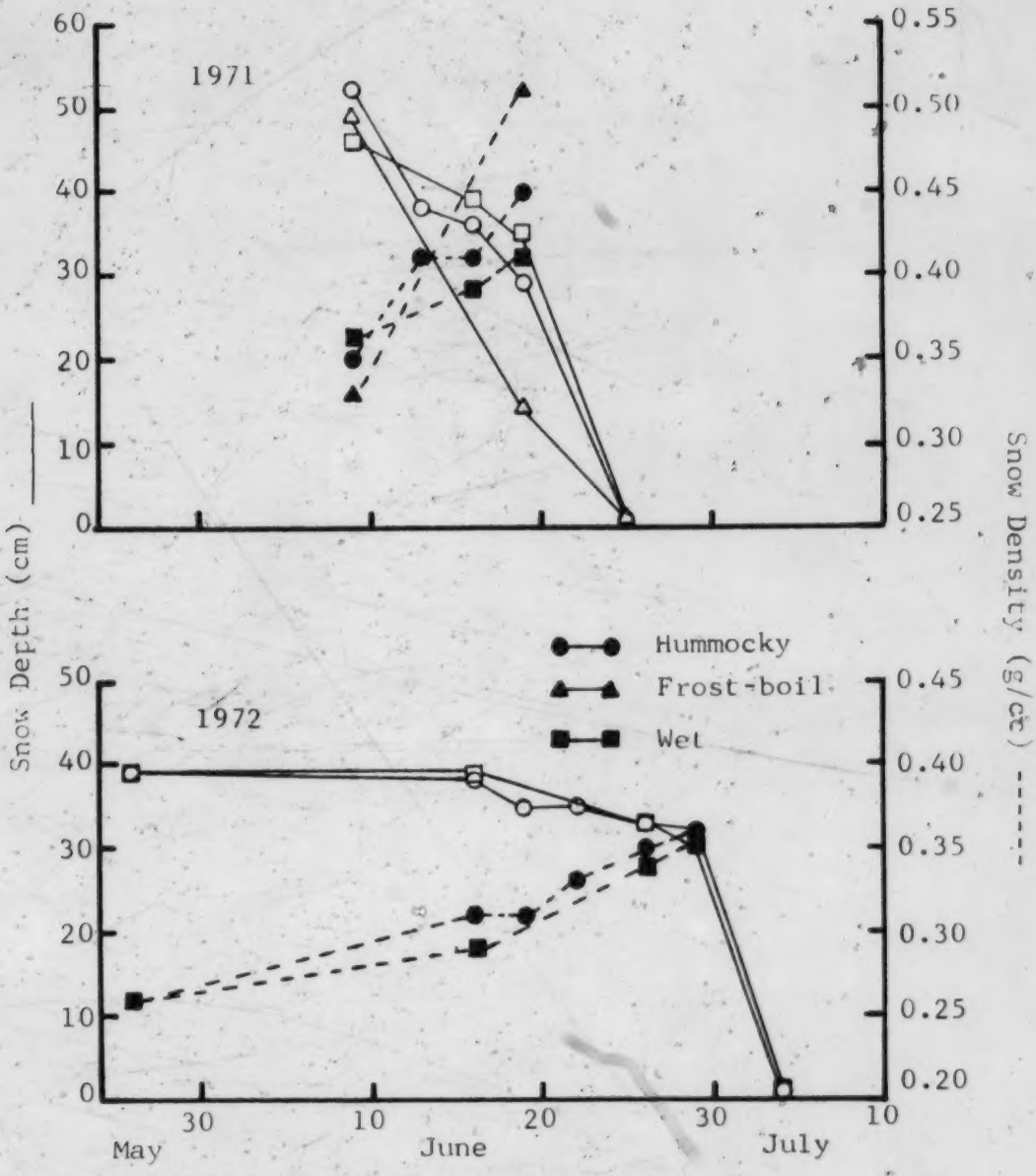

Figure 11. Snow depths (cm) and densities (g/cc) in a hummocky (site 1), frost-boil (site 13), and wet (site 18) sedge-moss meadow 1971, 1972.

sampling dates. During this interval, however, 10 cm of snowfall was recorded (Courtin 1973). Lowland meadow snowmelt ($\geq$ 50% surface area snow-free) occurred by June 28 (1970), June 25 (1971), July 4 (1972), and June 18 (1973). Early spring (May) snow densities averaged 0.26 g/cc and almost doubled to 0.44 g/cc a week before complete snowmelt (Fig. 11).

Active Layer

Meadow seasonal soil thaw (4-year interval) at the hummocky (site 1) intensive study meadow (Fig. 12) corresponded to seasonal incoming radiation and temperature regimes. Earlier and milder growing seasons (1971, 1973) had an average maximum thaw depth which was 8 cm deeper than that in a later and cooler season (1970, 1972). Meadow thaw over the first three weeks of the growing season was ca. 1 cm/day and subsequently decreased to ca. $\leq$ 0.5 cm/day until mid-August. Refreezing began to occur by late-August. Approximately 70 - 80% of the seasonal maximum thaw occurred three weeks after snowmelt.

Meadow soil thaw showed a variable inter-site relationship (Fig. 13). Deepest thaw occurred in meadows (sites 7,10, 13) with Gleysolic Static and Turbic Cryosols (fine textured mineral materials) and were substantially lower (50%) in meadows underlain by Fibric Organo Cryosols (peaty material).

Microtopographic (hummock, hollow, frost-boil) comparisons of seasonal (1972) soil thaw in the hummocky (site 1) and frost-boil (site 13) meadows (Fig. 14) showed distinctive

Figure 12. Seasonal thaw depth (cm) at the hummocky intensive study (site 1) meadow 1970 - 1973.

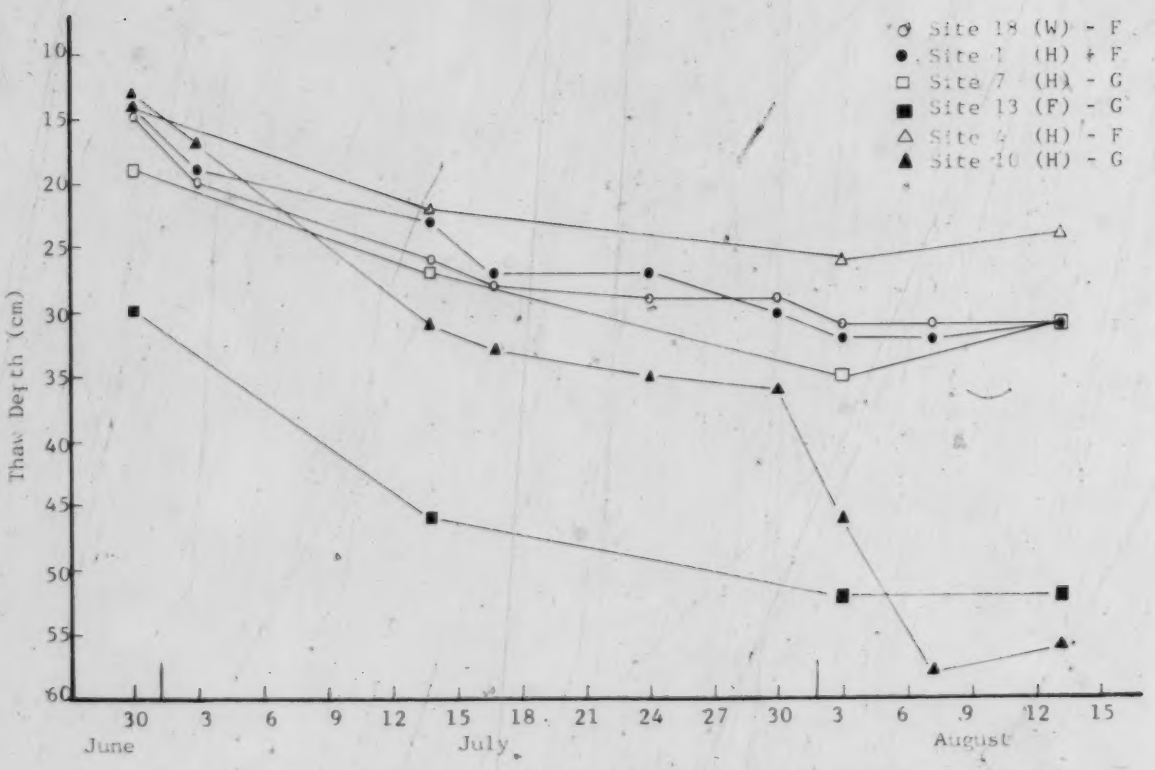

Figure 13. Seasonal thaw depths (cm) in 6 lowland sedge-moss meadows (H= hummocky, F= frost-boil, W= wet). Associated meadow soils (F= Fibric Cryosol, G= Gleysolic Cryosol) are indicated for each stand 1971.

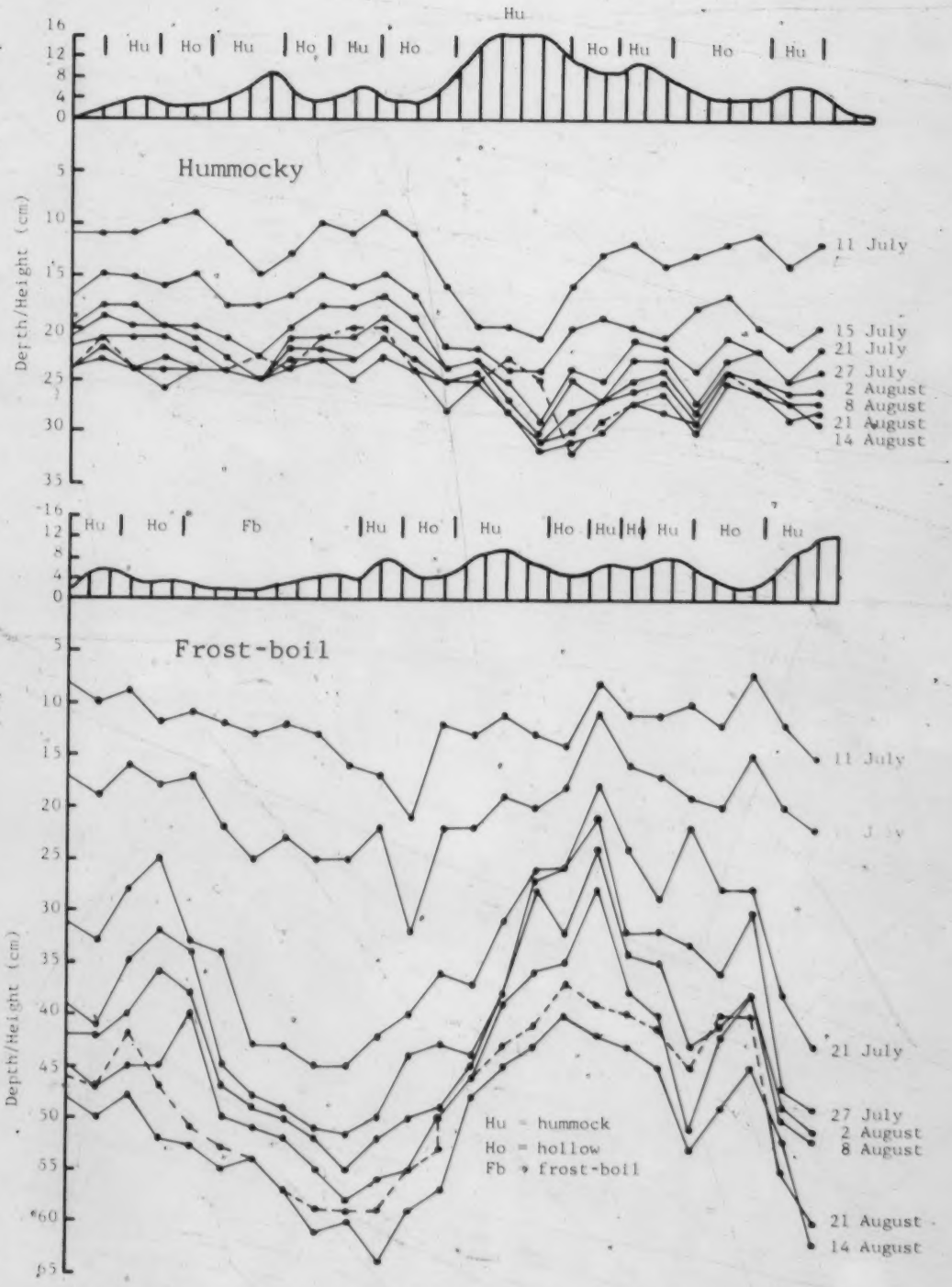

Figure 14. Seasonal soil thaw (cm) profiles beneath microhabitats (hummocks, hollows, and frost-boils) at the hummocky intensive study (site 1) and frost-boil (site 13) sedge-moss meadow 1972.

correlations. Thaw within a frost-boil was faster and deeper (11 - 24 cm) than under adjacent hummocks. The average maximum thaw depth in the frost-boil meadow was 50 cm. At the hummocky meadow the deepest thaw was found under well developed hummocks. Soil thaw was on the average 5 cm deeper than under adjacent hollows and 2 cm deeper than in poorly developed hummocks. In both the hummocks and hollows, the seasonal thaw pattern was more gradual than that found in frost-boils. The average maximum soil thaw depth in the hummocky meadow was 26 cm. Seasonal soil thaw development in the wet (site 18) meadow was less variable because of the flooded conditions and relatively homogeneous environment. The average maximum soil thaw depth for the wet meadow was 22 cm.

Temperature

Upper (10 cm) vascular plant canopy temperatures in the hummocky intensive study (site 1) meadow varied considerably from year to year (Fig. 15) but were only ca. 15% lower than those in the center (5 cm) of the plant canopy. Mean growing season temperatures ranged between 5 - 10° C in warmer years (1970, 1971, 1973) but were < 5° C in a colder year (1972). Above zero degree mean temperatures developed by mid- (1971, 1973) to late- (1972) June and continued into mid-August (1972) or mid-September (1971). Growing season temperatures at the moss/soil interface (-5 cm) were seasonally 2 - 5° C (8.5° C maximum) and were 1 - 4° C (5.5° C maximum) at the -10 cm soil depth (maximum rooting zone). Above zero degrees

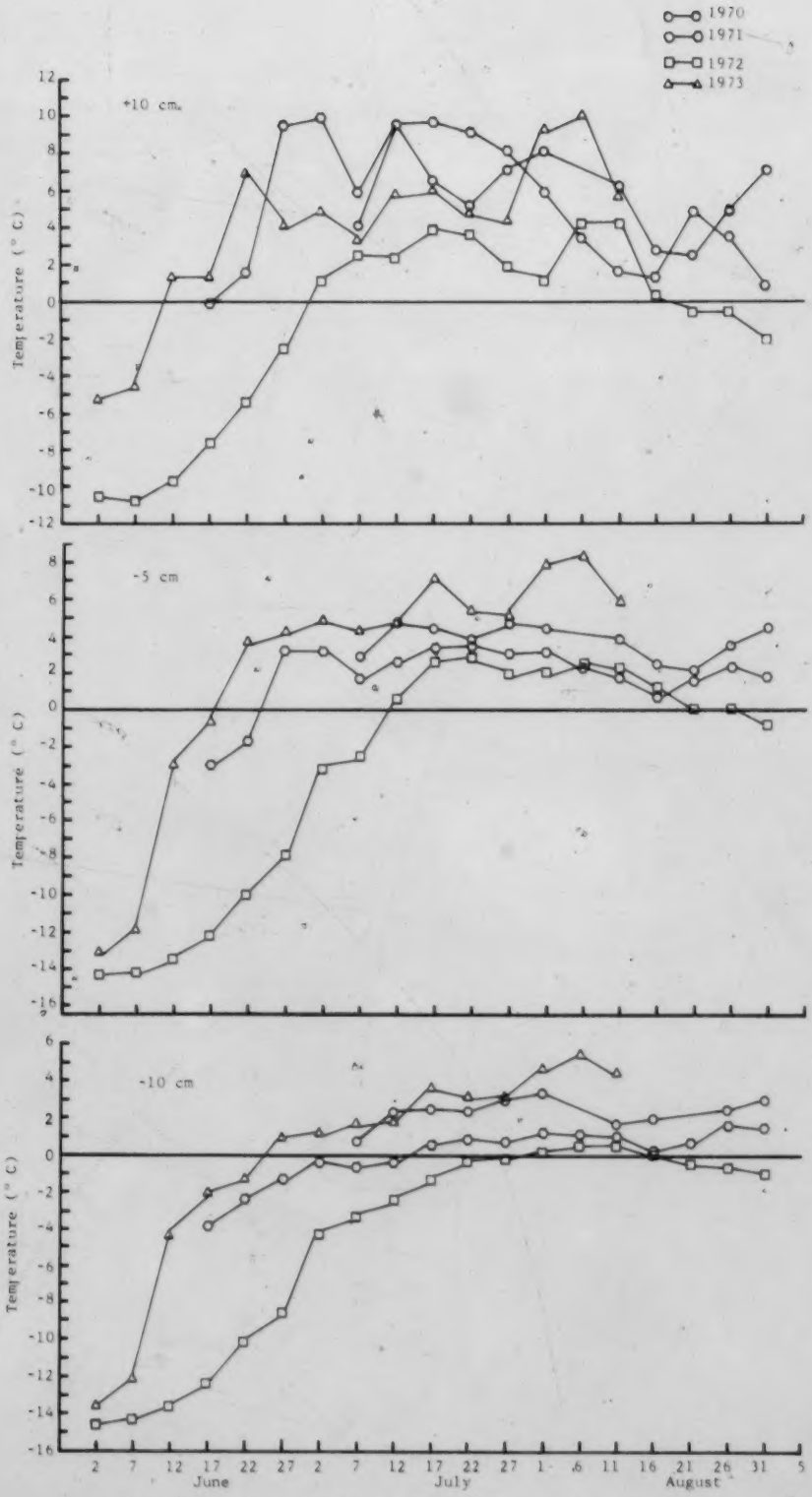

Figure 15. Seasonal (5 day means) temperature (° C) profiles for the hummocky intensive study (site 1) meadow 1970 - 1973 (data from Courtin).

temperatures in the soil (-5 cm) developed by mid- (1971, 1973) June to late-July (1972) and at a depth of -10 cm, not until late-June to mid-July (1971, 1973) or August (1972). Temperatures remained above zero degrees into mid-August to late-September (1971). Inter-site meadow temperature variation extremely variable (Table 6).

Table 6. Weekly mean hygrothermograph temperatures (°C) of three hummocky (sites 1,7,10) and one wet (site 18) sedge-moss meadow 1972 (compiled from Courtin 1973).

Site	Week Ending				
	12-June	3-July	24-July	14-August	21-August
Intensive study meadow (site 1)	-9.0	2.7	5.7	6.4	2.1
Coastal meadow (site 7)	-1.1	1.0	2.3	0.7	-0.7
Plateau-base meadow (site 10)	-4.3	1.8	4.4	3.8	1.8
Wet meadow (site 18)	...	...	3.8	...	...

The hummocky intensive (site 1) study meadow had the lowest (-9° C) and highest (6.4° C) seasonal temperatures recorded and was on the average 25% warmer than the plateau-base hummocky meadow (site 10). The single (3.8° C) wet (site 18) meadow temperature suggested an intermediate temperature regime to that of the two (sites 1,10) hummocky meadows.

Meadow Greenhouse Microclimate

Comparative mid-July to mid-August greenhouse and adjacent ambient temperatures are shown in Table 7. Greenhouse Carex stans leaf temperatures were approximately 60%

Table 7. Mean (±standard error) late July and early August *Carex stans* leaf, air (5 cm), moss (-1 cm), and soil (-10 cm) thermocouple temperatures (° C) (1100 - 1700 hr) in a field greenhouse and adjacent hummock and hollow habitats at the hummocky intensive study (site 1) meadow 1972.

Period	n	Greenhouse				Outside: Hummock				Hollow	
		leaf	air	moss	soil	leaf	air	moss	soil	moss	soil
July 15 - 31											
1100 - 1300	10	13.2	13.9	15.0	11.2	7.9	6.5	16.2	7.4	10.8	4.3
		±1.3	±1.1	±0.9	±1.6	±0.9	±0.8	±1.7	±1.0	±1.0	±0.8
1300 - 1500	6	18.2	17.1	17.7	7.1	11.1	9.3	18.4	10.5	13.2	6.4
		±3.4	±2.7	±1.4	±1.0	±2.3	±2.7	±1.3	±0.9	±0.9	±0.5
1500 - 1700	9	14.0	12.9	14.5	6.9	9.8	8.5	14.9	10.2	11.6	5.3
		±1.9	±1.8	±1.9	±0.6	±1.6	±1.4	±1.0	±0.8	±0.8	±1.8
Mean		15.1	14.6	15.7	8.4	9.6	6.1	16.5	9.4	11.9	5.3
August 1 - 12		9.3	11.3	11.4	4.0	5.7	5.3	9.9	4.7	6.5	3.3
1100 - 1300	6	±0.6	±0.9	±0.9	±1.0	±0.8	±1.3	±1.3	±0.9	±1.3	±0.8
1300 - 1500	4	10.5	11.9	13.1	4.0	5.9	5.8	13.0	5.5	9.9	3.9
		±1.0	±0.8	±1.5	±0.8	±0.7	±1.4	±1.6	±0.8	±1.1	±0.7
1500 - 1700	5	8.1	9.3	13.0	4.9	5.9	5.7	10.1	6.4	8.6	4.8
		±0.7	±1.1	±2.4	±0.4	±0.4	±0.7	±2.3	±1.1	±1.9	±1.0
Mean		9.3	10.8	12.5	4.3	5.8	5.6	11.0	5.5	8.3	4.0

greater than outside leaf temperatures and mid-canopy (5 cm) temperatures were 7° C higher (115%) than those outside the greenhouse. Average July sedge leaf temperatures of 15° C in the greenhouse and 6° C in the controls, were only 5 - 15% higher than canopy air temperatures. In early August the mean leaf temperatures in the greenhouse were 9° C and 6° C in the controls. These were 14% lower and 4% higher, respectively, than corresponding air temperatures. Greenhouse moss (hummock habitat) temperatures were slightly lower (5%) in July but higher (13%) in August, as compared to corresponding temperatures in the outside environment. Greenhouse soil (-10 cm) temperatures were 10 - 20% lower than those in outside hummocks.

Outside hummock moss temperatures were 36% higher than those in hollows. Hummock soil temperatures were 77% higher in July and 38% higher in August, compared to hollow temperatures. The warmest daily temperatures measured occurred between 1300 - 1500 hr. Mean early August temperatures were approximately 30% less than those recorded in July.

A mid-August continuous 24 hr temperature profile for the greenhouse and outside habitats is plotted in Fig. 16. Mean hourly below zero temperatures in the greenhouse plant canopy air, sedge leaf, and moss canopy were maintained from 800 - 2100 hr and corresponding outside air and sedge leaf temperatures as well as both greenhouse and outside soil temperatures showed a 2 - 3 hr lag. Peak air, sedge leaf, and moss temperatures devloped in both areas at

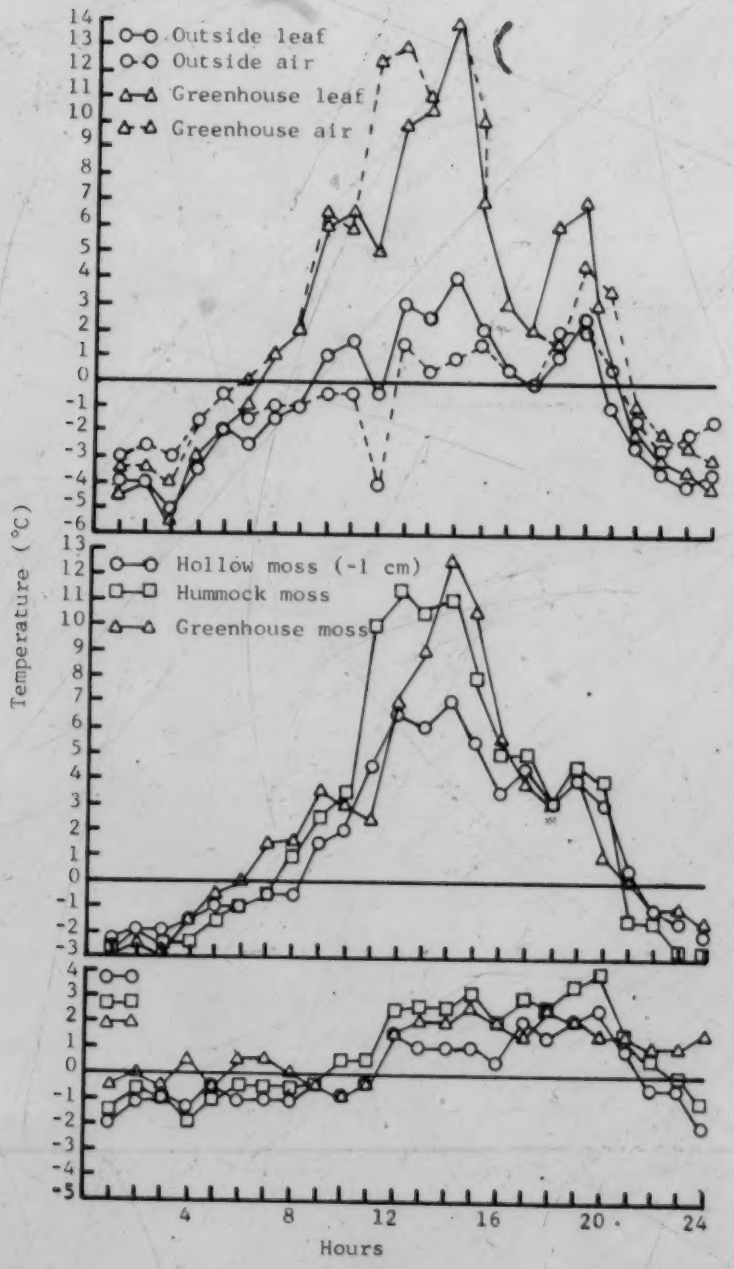

Figure 16. Thermocouple temperature profiles in various habitas of the hummocky meadow field greenhouse and adjacent (control) areas over a 24 hr interval on August 15 - 16 1972.

approximately mid-afternoon (1400 hr) and peak soil temperatures by early evening (2000 hr). Although greenhouse sedge leaf temperatures were from 15 - 250% higher than those of controls, the latter leaves still maintained their temperatures 50 - 300% higher than ambient air temperatures. Greenhouse leaf temperatures showed a very close correspondence to their ambient air temperatures. Below-freezing hummock and hollow temperatures were similar but above-freezing hummock moss and soil temperatures were approximately 35 - 70% higher than those in hollow habitats.

Discussion

Snow

Average 1971 late spring meadow snow depths were 45 cm and were 40 cm by mid-June in 1972. These were comparable to the 35 - 40 cm mid-June (1972) snow depths measured in lowland rock outcrop habitats (Bliss and Kerik 1973) but somewhat intermediate to the 25 cm (crest) to 60 cm (transition zone) snow depths measured on the raised beach intensive study site (Svoboda 1974). Snow accumulation in the transition zone of the raised beach was approximately 11 cm deeper than that in the adjacent frost-boil meadow. The deeper snow development in the former habitat would be due to snow drift accumulation. Benson and Brown (1970) found maximum snow depths on level (meadow ?) tundra areas in northern Alaska to be 46 cm.

The light (0.26 g/cc) late winter (May) snow density was representative of the winter snow cover. Such deep (39 cm)

and light snow was certain to provide an effective layer of insulation for the meadow vegetation. Courtin and Labine (1976) found that winter (1973) snow/moss layer temperatures in the meadow were 6 - 10° C higher than corresponding air temperatures above the snow. Lowland snowcover accumulation occurred by early September and deposition continued until early June (Courtin 1973). Snow accumulation in the January-March (1973) period was minimal (Courtin and Labine 1976) and indicated that maximum snow accumulation was primarily an early and late winter development.

Late spring snowmelt and dates of total snowmelt were regulated by incoming solar radiation levels. The cloudier spring conditions in 1972 reduced incoming solar radiation levels below those for the comparable 1971 period (Courtin and Labine 1976). Total snowmelt in 1972 was therefore a week later and not as progressive as it had been in 1971. Maximum annual variation in the time of total meadow snowmelt was approximately two weeks (June 18 - July 4). The increasing water content of snow prior to complete melt and the associated freeze/thaw temperature conditions, were important factors in litter formation and sub-snowsurface vascular plant growth. The latter was possible because of the creation of miniature 'ice greenhouses'. These two topics are discussed in their respective sections. Meadow pre-snowmelt snow densities of 0.4 - 0.5 g/cc were similar to those measured on the raised beach (Svoboda 1974).

Active Layer

The average annual maximum meadow thaw was 56 cm in the frost-boil meadow; 28 cm in the hummocky meadow; and 27 cm in the wet meadow (Table 8).

Table 8. Mean maximum seasonal soil thaw depths (cm) in three lowland sedge-moss meadows 1970 - 1973.

Meadow	Site	1970	1971	1972	1973	Mean
Frost-boil	13	...	58	50	59	56
Hummocky	1	23	32	26	31	28
Wet	18	...	30	22	29	27

Thaw was 10 cm deeper in an earlier and milder season (1971, 1973) and reflected higher incoming radiation levels and the associated increases in temperature. This yearly variation in incoming radiation and temperature caused the thaw depth to annually vary by ca. 15% at the frost-boil meadow and by 30% at the hummocky and wet meadows. At lower soil depths (20 - 25 cm) thaw occurred for only a portion (ca. 50%) of the growing season. Major meadow rooting concentrations (Dennis and Johnson 1970, Muc 1976) and microbial populations (Widden 1976) were found in the upper 5 - 20 cm of the soil profile.

Rapid (1 cm/day) soil thaw in the lowland meadows was associated with high (0.3 - 0.5 ly/min.) incoming solar radiation levels (Courtin and Labine 1976). Such early season soil thaw was also found in low arctic meadows (Haag and Bliss 1974). Freezing of the meadow soil initially

(mid-August) began from the bottom up and coincided with radiation levels < 0.2 ly/min. Meadow soils were completely refrozen by mid-September (Brown 1976).

Meadow soil thaw depth was also influenced by soil: i) composition; ii) organic matter content; iii) moisture content; and iv) vegetation cover. The deep thawing frost-boil (site 13) and hummocky (sites 7, 10) meadows were underlain by Gleysolic Cryosols (Walker and Peters 1976). These soils consisted of an organic surface layer over finely textured mineral material. The meadow vegetation cover was unequal in its distribution and the soil moisture (oven-dry) content was < 100%. Under such conditions, less heat was required to melt the low soil ice content and subsequently greater thaw depths developed. Haag and Bliss (1974) reported a similar association between soil thaw depth and mineral composition, in a low arctic meadow. Shallower soil thaw in the coastal hummocky (site 7) meadow with a Gleysolic Static Cryosol, was influenced by the site's close proximity to the cold ocean waters and the accumulations of shoreline ice.

The hummocky (site 1) and wet (site 18) meadow Fibric Organo Cryosols (Walker and Peters 1976) were supersatureated (> 340% oven-dry) peaty soils which were overlain by an extensive and lush plant canopy. The resulting greater insulation provided by the vegetation and the soil's higher ice content, reduced their thaw depth to approximately half that found in the Gleysolic Cryosols. Addison (1976)

found the hummocky (site 1) meadow vegetation intercepted the majority of the incident radiation and reduced the soil heat flux by 50%. Comparable patterns of meadow soil thaw variability, reflecting different soil conditions, have also been described from Eurasian sites (Khodachek 1969, Pavlova 1969).

Frost-boils, hummocks, and hollows are distinctive biological meadow microhabitats. The warmer, better-drained, and potentially more nutrient rich hummocks were preferential vascular plant growth habitats. Conversely the higher soil alkalinity, lower moisture content, and greater activity of the frost-boil soils, reduced their growth habitat potential for vascular species. In the frost-boil meadows, the vegetation was concentrated in areas of soil organic matter accumulation and the vascular plant cover of frost-boils was only 10 - 15%.

Temperature

No pronounced vertical aboveground temperature gradient was found in the lowland meadows. Temperatures 100 - 200 cm above the plant canopy were only 2 - 3° C lower than those at a height of 10 cm (plant canopy). Low (1 - 2.4 m/sec.) meadow wind speeds (Courtin 1972); an open environment; and low vegetation cover, were instrumental in the lack of vertical temperature gradation. Although the seasonal mean canopy temperatures were < 10%, Mayo *et al.* (1976) found the sedge plants adapted to photosynthesize at lower temperatures. Substantial (50 - 100%) increases in sedge photosynthesis

were found (Mayo et al. 1976) with temperature increases of 0 - 5° C. Tieszen (1970) reported similar findings for low arctic meadow monocots.

Bliss (1975) calculated the average (1971 - 1973) lowland meadow accumulated degree days above zero (at 10 cm) to be 309 and to range from a high of 443 in an earlier and milder season (1971) to a low of 137 in a later and cooler season (1972). Each year, favorable above zero degree air temperatures were maintained 2 - 3 weeks beyond the peak of the growing season. This suggested that temperature alone was not controlling plant growth but that a multiple of factors were involved.

Development of mean above zero degree meadow soil temperatures lagged by approximately two weeks but was offset by their longer (two week) duration at the end of the season. The onset of the growing season was seasonally more variable than was the onset of dormancy. This resulted from a more significant variability in climatic reduction (clouds etc.) of incoming radiation in the early part of the growing season (Courtin and Labine 1976).

Low, mean belowground meadow temperatures (1 - 4° C) were found within the most active rooting zone (10 cm). Temperatures 5 cm above this zone were only 1° C warmer but possessed a greater (40 - 200%) maximum temperature regime. The low meadow soil temperatures and corresponding low oxygen tensions created by saturated soil conditions, produced a stressful growth environment. Addison (1976)

found Carex stans periodically experiencing water stress conditions as severe as those in Dryas integrifolia on the raised beaches. Root growth did not appear to be critically affected by the low meadow temperatures. Billings et al. (1973) found low arctic Eriophorum angustifolium to maintain root growth at temperatures as low as 0.5° C and Carex aquatilis (low arctic equivalent of C. stans) to concentrate its root growth at slightly higher temperatures. Undoubtedly the pronounced vertical root stratification found in arctic meadows (Dennis and Johnson 1970, Muc 1976) corresponds to the stratified soil temperatures.

Low mean seasonal aboveground temperatures at the coastal hummocky (site 7) meadow were a reflection of the cold marine environment near-by. Similarily the lower plateau-base hummocky (site 10) meadow temperatures were influenced by the presence of extensive permafrost formation under the plateau. Rock outcrop associated meadows such as the hummocky intensive study (site 1) meadow were generally warmer because of the reradiation from the granitic rocks (heat sinks).

Meadow physiography and vegetation cover were influential in the development of soil temperature regimes. Pavlova (1969) found temperatures of mineral meadow soils to be 40 - 50% higher than those in adjacent peaty soils. Similarily Vassiljevskaya et al. (1972) found West Taimyr meadow soil temperatures beneath extensively vegetated areas to be lower and to vary less on a daily basis, than those

under poorly vegetated areas. This would indicate that the warmest lowland meadow soil conditions would develop in the Gleysolic Turbic Cryosols and the coldest conditions in the Fibric Organo Cryosols.

Meadow Greenhouse Microclimate

Average field greenhouse canopy temperatures were 7° C warmer than those outside the greenhouse. Svoboda (pers. comm.) found raised beach greenhouse air temperatures to be 6.5° C warmer whereas Tieszen (1971) found them to be only 3° C warmer in the Barrow meadow greenhouse. Greenhouse sedge leaf temperatures were 4.5° C higher than those of the controls but both sets of leaf temperatures were only slightly (5 - 15%) higher than surrounding air temperatures. Seasonal meadow air temperature regimes were a close indication of the seasonal sedge leaf temperatures and corresponding photosynthetic capacities. Warmer outside hummock moss (36%) and soil (58%) temperatures were a reflection of better soil drainage and more efficient interception of incoming solar radiation, by these habitats. Consequently plant cover on the hummocks was more luxurious than in the hollows.

The lower average August temperatures corresponded to decreasing incoming radiation levels (Courtin and Labine 1976). A distinctive day and night tempertature regime devloped in the meadows by mid-August. Air temperatures were above zero for only half of the day and did not exceed 4° C. Although Mayo et al. (1976) reported Carex

stans as capable of photosyntheszing at low temperatures; photosynthetic rates did show a pronounced (ca. 40 - 80%) decrease during the evening hours when solar radiation levels had decreased substantially. Decreasing solar radiation and temperature regimes in early- to mid-August would serve as effective 'cues' in initiating vascular plant dormancy in the lowland meadows.

SOILS

Shallow and weakly developed profiles, an underlying permafrost table, and associated patterned ground features are characteristic of arctic soils. Although the availability of loose marine, lacustrine, alluvial, and aeolian deposits have partially compensated for reduced rates of mechanical and chemical weathering, arctic pedogenic processes operate at extremely slow rates. James' (1970) study on two separate Rankin Inlet (N.W.T.) soils which had an age difference of 4000 years, revealed no pronounced pedogenic difference.

The major arctic soil groups reported in the literature, were the lithosols, regosols, Arctic browns, tundra, and bog soils. The first four are of mineral composition and the last two are organic soils. Tundra soils have been further divided into upland and meadow tundra groups (Brown 1969).

Russian pedologists designated the major arctic soils as gleysols to peaty-gleysols and classified them as azonal or hydromorphic soils (Liverovskii 1964). Tundra soils were also considered to be counterparts of temperate zone gleysols

and the Arctic brown soils as being equivalents of podzols (Tedrow and Cantlon 1958).

Previous descriptions (King 1969, Barrett 1972) of the Truelove Lowland soils used the American system of arctic soil classification extensively used by Tedrow, Brown, and others. Walker and Peters' (1976) lowland soils studies in the IBP project used a comparative classification system consisting of the Canadian Systems of Soils Classification, the 7th Approximation, and the 'Tentative Classification for Arctic Soils'. This latter experimental classification was developed by Tarnocai, Pettapiece, and Zoltai (1973) and was distributed in memorandum form by J.A. McKeague of the Soils Research Institute, Ottawa. It is this nomenclature system that is used in this thesis.

Land form features, drainage patterns, soil texture, and soil composition, were the major features differentiating the lowland soils. The soil data reported in this thesis were collected in the 20 lowland meadow stands used for phytosociological studies. Field profile descriptions were made in each stand and limited soil physical analyses made on representative material from a stand of each meadow community type. Comparative meadow nutrient and physical property data were already available (Peters and Walker 1972, Walker and Peters 1976) for a number of lowland meadows.

Methods

Within each meadow stand studied, a soil pit was dug

down to the permafrost table under each distinctive meadow microhabitat (frost-boil, hummock, hollow). For each profile horizon — thickness, moist color (Munsell), rooting intensity, and soil texture was described. Depth (cm) to the frozen portion of the active layer was also measured.

In 1971, gravimetric soil moisture determinations were made on soils from the hummocky intensive study (site 1), frost-boil (site 13), and wet (site 18) meadow. Weekly sampling consisted in the collection of triplicate core (6.5 cm diameter) samples taken to the frozen active layer. The cores were divided into 5 cm segments and their soil moisture content was expressed on an oven-dry (105° C for 24 hr) basis. Weight/volume calculations provided soil bulk density data. Soil pH determinations were made on samples collected in mid-season (July 17). A 1:2 soil water ratio was used for rewetting (24 hr) the samples and readings taken on a Sargent model PBL pH meter.

Meadow topographic (hummocks, hollows, frost-boils) area distributions were calculated from tape transects used in a frost-boil (site 13) and hummocky (site 1) meadow. Ten 25 meter long transects were laid out in a north - south orientation and at 5 meter intervals from one another, in each meadow stand. The extend of coverage by each topographic unit was recorded in each transect and averaged for the stand. Similar topographic distribution information was gathered in the remaining 18 stands by means of 20 X 50 cm quadrats (n= 10 - 16).

Results

Frost-boil Sedge-moss Meadows

Frost-boil meadows were generally found adjacent to raised beaches or in areas of extensive alluvial deposition. Open frost-boils (mud boils), with an average surface area cover of 42±1.9%, were their major characteristic feature. The remaining 58±1.9% of the meadow surface was covered by hummocks (35%) and hollows (23%). Hummocks, similar to those of the hummocky meadows, ranged from 7 - 14 cm in height and from 10 - 80 cm in diameter. The majority of the lowland frost-boils had a relatively flat to slightly concave surface and were overlain by a thin (ca. 1.5 cm) algal-moss mat. The vascular plant cover of the frost-boils was 10 - 15% (Fig. 17).

Organic matter accumulation varied with the topography and vegetated areas (hummocks and hollows) possessed the highest concentrations and frost-boils the lowest. The more extensive plant growth and organic matter buildup was often around protruding or subsurface boulders. The basement layer of the thawed soil consisted of greyish-brown sandy loam.

Two basic soils were found in these meadows. Heavily vegetated areas were underlain by Gleysolic Static Cryosols similar to those of hummocky meadows. The following is a description of a Gleysolic Static Cryosol beneath a hummock and hollow habitat:

Figure 17. A relatively inactive frost-boil (foreground) showing evidence of a vascular plant cover development.

Habitat	Layer	Depth (cm)	Description
Hummock	1	0 - 3	live moss, vascular plant stems, litter.
	2	3 - 7	dead moss and vascular plant stems, roots and rhizomes.
	3	7 - 24	very dark brown (7.5 YR 2/2) organic matter with abundant rooting.
	4	24 - 32	very dark brown (7.5 YR 2/2) sandy loam, stony, and with plentiful rooting.
	5	32 -	frozen portion of the active layer.
Hollow	1	0 - 2	live moss, vascular plant stems, and litter.
	2	2 - 5	dead moss and vascular plant stems, roots, rhizomes.
	3	5 - 15	very dark brown (7.5 YR 2/1) organic matter with abundant rooting.
	4	15 - 25	very dark greyish-brown (10 YR 3/2) sandy loam, stony, and with plentiful rooting.
	5	25 -	frozen portion of the active layer.

Frost-boils had Gléysolic Turbic Cryosols, with the following description:

Habitat	Layer	Depth (cm)	Description
Frost-boil	1	0 - 0.5	live moss, algae, and litter.
	2	0.5 - 1.5	dead moss and algae.
	3	1.5 - 9.5	dark brown (10 YR 3/3) sandy loam with few roots.
	4	9.5 - 42	yellowish-brown (10 YR 5/4) sandy loam with few roots.
	5	42 -	frozen part of the active layer.

The fine sandy loam texture, low organic matter content, and reduced soil moisture content of these soils resulted in their thaw being 10 - 17 cm deeper than that in adjacent Gleysolic Static Cryosols. Mechanical analyses of a frost-boil soil revealed a 47% sand, 35% silt, and 18% clay content in the upper 38 cm of the profile and a 79% sand, 16% silt, and 5% clay content in the lower 47 cm of the profile (Peters and Walker 1972).

Hummocky Sedge-moss Meadows

The hummocky meadows feature a characteristic hummock/hollow topography. On the average, 61%±8.5% of their surface area is covered by hummocks and 39±8.5% by hollows. Hummocks ranged in size from 5 - 15 cm in height and from 15 - 90 cm in diameter. The hummocks, according to Raup's (1965) classification, are moss derived and developed on slightly elevated mounds of organic material overlying a peaty mineral substratum.

Hummocky meadows were underlain by either Gleysolic Static Cryosols (60% of the stands) or by Fibric Organo Cryosols (40% of the stands). The following is a description of a Gleysolic Static Cryosol beneath a hummock and hollow:

Habitat	Layer	Depth (cm)	Description
Hummock	1	0 - 2	live moss, vascular plant stems, and litter.
	2	2 - 7	dead moss, vascular plant stems, roots and rhizomes.
	3	7 - 13	very dark brown (7.5 YR 2/2) organic matter with abundant rooting.

Habitat	Layer	Depth (cm)	Description
	4	13 - 23	very dark greyish-brown (2.5 Y 3/2) sandy loam with plentiful rooting.
	5	23 -	frozen part of the active layer.
Hollow	1	0 - 2	live moss, vascular plant stems, roots, and rhizomes.
	2	2 - 7	dead moss, vascular plant stems, roots, and rhizomes.
	3	7 - 14	very dark brown (10 YR 2/3) organic matter with abundant rooting.
	4	14 - 18	very dark grey brown (2.5 Y 3/2) sandy loam with plentiful rooting.
	5	18 -	frozen part of the active layer.

The following is a description of a Fibric Organo Cryosol beneath a hummock and hollow:

Habitat	Layer	Depth (cm)	Description
Hummock	1	0 - 2	live moss, vascular plant stems, and litter.
	2	2 - 5	dead moss, vascular plant stems, roots, and rhizomes.
	3	5 - 15	dark reddish-brown (5 YR 3/4) organic matter with abundant rooting.
	4	15 - 19	dark brown (7.5 YR 2/3) organic matter with abundant rooting.
	5	19 - 24	dark reddish-brown (5 YR 3/4) organic matter with abundant rooting.
	6	24 - 31	dark brown (7.5 YR 2/3) sandy loam with abundant rooting.
	7	31 -	frozen part of active layer.

Habitat	Layer	Depth (cm)	Description
Hollow	1	0 - 4	live moss, vascular plant stems, litter.
	2	4 - 7	dead moss, vascular plant stems, roots, rhizomes.
	3	7 - 11	dark reddish-brown (5 YR 2/2) organic matter with abundant rooting.
	4	11 - 13	dark brown (7.5 YR 4/3) organic matter and sand with with abundant rooting.
	5	13 - 17	dark reddish-brown (5 YR 2/2) organic matter with abundant rooting.
	6	17 -	frozen part of active layer.

Meadows with the latter soil were generally better drained while meadows with the Gleysolic Static Cryosols were associated with poor drainage. Greater hummock area development was found in the meadows with Gleysolic Static Cryosols (64% surface area) than in the meadows with Fibric Organo Cryosols (56%).

Wet Sedge-Moss Meadows

Wet meadows were characteristically found in areas of impeded drainage (flooding) along streams, and pond margins. Reduced decomposition rates in these flooded habitats, added to the lush vascular and moss plant growth, resulted in extensive peat accumulations (50 cm deep). From 40 - 50% of the peat remained frozen within the permafrost. Fibric Organo Cyrosols, similar to those of the hummocky meadows, was found in these meadows.

The following is a description of a Fibric Organo Cryosol:

Layer	Depth (cm)	Description
1	0 - 4	live moss, vascular plant stems, and litter.
2	4 - 8	dead moss, vascular plant stems, roots, rhizomes.
3	8 - 13	very dark brown (7.5 YR 2/1) organic matter with abundant rooting.
4	13 - 24	dark reddish-brown (5 YR 3/2) organic matter with abundant rooting.
5	24 -	frozen part of active layer.

Soil Physical Properties

Average soil pH in the upper 25 cm of the profile showed a transition from acidic conditions in the Fibric Organo Cryosols to alkaline conditions in the Gleysolic Turbic Cryosols (Table 9). The Gleysolic Static Cryosols had an almost neutral soil pH. A drop in the soil pH at the 5 - 10 cm depth in the Fibric Organo Cryosol from the hummocky meadow and a similar drop in the Fibric Organo Cryosol (15 - 20 cm dpeth) of the wet meadow, indicated an accumulation of humic (acidic) compunds at these levels. The alkaline pH at the lower depths (15 - 25 cm) in the Gleysolic Static Cryosol of the frost-boil meadow, indicated the calcareous nature of the underlying sediments. The lower pH in the upper soil profile indicated organic matter accumulation and decomposition.

Table 9. Soil pH and bulk density (g/cc) along 5 cm depth intervals (n=3) in soils of a hummocky (site 1), frost-boil (site 13), and wet (site 18) sedge-moss meadow 1971.

Soil Depth (cm)	Frost-boil Meadow Gleysolic Turbic Cryosol		Gleysolic Static Cryosol		Hummocky Meadow Fibric Organo Cryosol		Wet Meadow Fibric Organo Cryosol	
	pH	BD	pH	BD	pH	BD	pH	BD
0 - 5	7.8	1.11	6.7	0.22	6.1	0.14	5.8	0.07
5 - 10	7.8	1.23	6.6	0.24	5.7	0.19	6.0	0.09
10 - 15	7.6	1.24	6.4	0.27	6.1	0.21	5.9	0.14
15 - 20	7.7	1.25	7.5	1.31	6.0	0.22	5.5	0.19
20 - 25	7.8	1.32	7.6	1.34	6.0	0.21	5.6	0.24
Mean	7.7	1.23	7.0	0.68	6.0	0.19	5.8	0.15

Low soil bulk density values (Table 9) in the Fibric Organo Cryosols of the hummocky and wet meadow and in the upper 15 cm of the Gleysolic Static Cryosol of the frost-boil meadow, indicated the peaty nature of the soil. The increase in soil bulk density at the lower depths of the Fibric Organo Cryosols was attributed to organic matter compaction and mineral matter (aeolian and alluvial) accumulation. The Gleysolic Turbic and Static Cryosols were primarily of mineral composition in the lower (15 - 25 cm) portion of their profile and revealed no organic matter inclusions.

Saturated soil conditions existed in all of the lowland sedge-moss meadows. Soil moisture levels in the frost-boil (site 13) meadow ranged from 50 - 70% in the frost-boils to 250 - 350% under the heavily vegetated areas. Soil moisture content of the hummocky (site 1) meadow ranged from 275 - 400% and was 350 - 525% in the wet (site 18) meadow. Soil moisture levels remained relatively stable over the course of the growing season.

Discussion

The weak and slow pedogenic development of arctic meadow soils was in large part a result of the low soil temperatures; short period of thaw; and high soil moisture content. Lowland meadow soils varied from deep thawing and poorly vegetated Gleysolic Turbic Cryosols to shallow thawing but well vegetated Fibric Organo Cryosols. The Gleysolic Static Cryosols, with characteristics inter-

mediate to those of the aforementioned soils, were the dominant lowland meadow soils.

Gleysolic Turbic Cryosols presented an extremely unstable rooting habitat because of potential cryoturbation. These soils also lacked a substantial organic matter content and were low in available nutrients (Walker and Peters 1976). The small (< 15%) vegetation cover which developed on them was initiated from bordering patches of dense vegetation. Walker and Peters (1976) described their development as being associated with poorly drained depressional areas with undifferentiated materials.

The Gleysolic Static Cryosols provided a suitable rooting habitat. Root biomass within these soils was only 30% of the biomass found in the Fibric Organo Cryosols. Meadows with the Gleysolic Static Cryosols possessed poor drainage and were associated with the coastal or plateau-base regions of the lowland. Courtin and Labine (1976) found the coastal (site 7) and plateau-base (site 10) hummocky meadows to be colder than the more inland hummocky intensive study (site 1) meadow which was underlain by a Fibric Organo Cryosol. The cold marine and plateau environments were considered as responsible for the lower temperatures of these meadows. Nitrogen fixation in the Gleysolic Cryosols was low (Stutz 1976) and would suggest that their nutrient levels might also be low.

The Gleysolic Static Cryosols developed on coarse to finely textured materials of alluvial flood plains or

drainage slopes (Walker and Peters 1976)

Gleysolic Cryosol types of soils have been widely reported from other high arctic areas. Those on Northern Ellesmere Island have been described as rego humic gleysols (Day 1964) and as tundra gleys on Cornwallis Island (Cruickshanks 1971). In the Low Arctic, Janz (1972) described such soils as cryic gleysols. Equivalent Eurasian soils are termed peaty gleys (Derviz-Sokolova 1966, Pavlova 1969, Tikhomirov 1969).

The Fibric Organo Cryosols provided the best growth medium for the meadow plants. Their average root biomass was 110 - 210% greater than that of Gleysolic Static Cryosols and meadows with these soils tended to possess a rich diversity of species. The available soil nutrients were 10 - 700% higher than those in the Gleysolic Static Cryosols (Walker and Peters 1976). Available phosphorus levels were low, a condition typical of organic soils and resulting from low decomposition rates. Stagnant water conditions in the Fibric Organo Cryosol soil of the wet (site 18) meadow resulted in low nitrogen fixation rates (Stutz 1976). The better drained Fibric Organo Cryosol of the hummocky intensive study (site 1) meadow had high nitrogen fixation rates and potentially a more favorable nutrient regime.

Walker and Peters (1976) found the Fibric Organo Cryosols developing on undifferentiated, very poorly drained depressional land forms. Comparable soils on Cornwallis

Island were described as bog soils (Cruickshanks 1971) and cryic fenno fibrisols in low arctic meadows (Jànz 1972).

Similar hummock dimensions in the hummocky and frost-boil meadow indicated similar ontogenies. Lowland meadow hummocks were only half the height of low arctic hummocks (Hopkins and Sigafoos 1950). A closer similarity was found with hummocks on northern Ellesmere (Savile 1964) and in Eurasian meadows (Khodachek 1969, Pavlova 1969, Beschel and Matveyeva 1972). Lowland meadow surface area coverage, by hummocks, of 56 - 64% were almost double those reported for Western Taimyr meadows (Beschel and Matveyeva 1972) but similar in extent to those of dryad-sedge-moss hummocky tundra (Khodachek 1969). Hummock formation and classification have been well documented (Hopkins and Sigafoos 1951, Raup 1965, Webster and Sharp 1973).

The average cover by frost-boils, in the lowland frost-boil meadows, was 42% of the total meadow area. The cover was 40 - 740% greater than that reported for low arctic meadows (Johnson et al. 1966, Pavlova 1969, Aleksandrova 1970a). In 'older' (less active) frost-boil meadows, frost-boils covered only ca. 20% of the surface area and possessed considerably greater ca. 50% plant cover. Lowland frost-boils had only 2.5% of the organic matter content of adjacented heavily vegetated areas (Walker and Peters 1976). Eurassian tundra frost-boils had 2 - 3 times less organic matter content than did comparable heavily vegetated areas (Grishna and Virchenko 1972). The low soil organic content and higher

surface area cover by frost-boils, suggested a more active set of conditions prevailing in the lowland frost-boil meadows. The development and activity of frost-boils has been well documented (Hopkins and Sigafoos 1951, Drury 1962).

A distinctive soil physical and chemical gradient occurred in the meadow soils (Table 10).

Table 10. Comparison of mean (n=15) soil physical and chemical properties (25 cm total depth) of three major sedge-moss meadow soils.

Soil	Meadow	pH	Bulk Desnity (g/cc)	Soil Moisture (%)	Max. Thaw (cm)
Fibric Organo Cryosol	wet	5.8	0.15	447	22
Fibric Organo Cryosol	hummocky	6.0	0.19	340	23
Gleysolic Static Cryosol	frost-boil	7.0	0.68	284	36
Gleysolic Turbic Cryosol	frost-boil	7.7	1.23	65	56

The Fibric Organo Cryosols were the most acidic and wettest meadow soils. They also possessed the lowest soil bulk densities. Gleysolic Turbic Cryosols had the heaviest and most alkaline soil conditions and their moisture content was only 15 - 25% that of other meadow soils. Average soil properties of the hummocky (site 1) and wet (site 18) meadow Fibric Organo Cryosol soil were similar, with the exception of the higher (25%) soil moisture content of the wet meadow soil. The Gleysolic Static and Turbic Cryosols

possessed the greatest soil property variation. The latter soil had an 80% higher bulk density and a 55% deeper thaw than did the Gleysolic Static Cryosol. Its soil moisture content was only 20% of that in the Gleysolic Static Cryosol. The increased pH at the lower depths, in the Gleysolic Static Cryosol, corresponded with Peters and Walker's (1972) findings of decreasing organic matter content with depth. Soil density data did not indicate an accumulation of buried organic matter within either of the Gleysolic Cryosols. The increased soil density, with depth, in the Fibric Organo Cryosols indicated a compaction and sedimentation of materials in the lower soil profile. This would be a further limitation to rooting at the lower soil depths.

PHENOLOGY AND PLANT GROWTH

Seasonal meadow phenology and growth patterns provide an insight into the adaptive survival strategies of arctic plants. Plant growth dynamics are additionally reflected in seasonal community chlorophyll levels, leaf area, carbohydrate and biomass patterns. Arctic plant growth has also adapted itself to a short growing season and has become highly efficient inthis respect.

Phenological and growth measurement (phenometric) data, collected from the dominant meadow species (primarily Carex stans), made it possible to examine inter-seasonal and inter- and intra-site variability in plant growth. Seasonal total plant photosynthetic shoot length increment data and post

growth-peak dieback data made it possible to correct for aboveground primary production underestimates.

Methods

Plant Growth

In 1970, phenology and growth measurements were taken from Carex membranacea at the hummocky intensive study (site 1) meadow. In 1971, these measurements were extended to include Eriophorum angustifolium, Arctagrostis latifolia, Pedicularis sudetica, Polygonum viviparum, Salix arctica and Carex stans. Measurements were also made on C. stans at the wet (site 18) meadow. In 1972, data were only gathered from C. stans at the hummocky and wet meadows and from Carex membranacea at the hummocky and frost-boil (site 13) meadows. In each meadow, exclusive of the wet meadow, the sedges were studied separately in the hummock and hollow habitats. Leaf increment measurements were also collected from C. stans plants in the field greenhouse.

Growth measurements of the above plants were based on individual leaf photosynthetic tissue increment. In Salix arctica, the seasonal photosynthetic leaf length of a select number (n=10) of leaves per plant, was measured. Ten plants per species were found to be sufficient to provide a measurement variability of ±10%. Each tiller's stem base was tied with a sewing thread immediately above the moss surface. On each leaf, the photosynthetic terminal point was marked with India ink (0 pen) and regular measurements (mm) taken of the distance between these two reference points. Records

were also kept of the dates of leaf and floral initiation as well as the time of seed set. These observations were taken on both tagged and untagged plants. Leaf increment measurements were taken every two days in 1970; every three days in 1971, and every five days in 1972.

Potential sub-snowsurface sedge leaf growth was measured in three ways:

1. Late fall (1971) tagging and measuring of ten Carex stans tillers at both the hummocky (site 1) and wet (site 18) meadows. Tillers were remeasured, immediately after thaw, the next spring.

2. Uncovering and tagging ten C. stans plants in May 1972 and then recovering the plants with snow. Measurements were taken immediately after snowmelt in July.

3. A 1 meter square area of the hummocky intensive study (site 1) meadow was cleared of its snow cover (30 cm) in late spring (June 22) 1972 and 15 C. stans tillers were tagged. The tillers were left uncovered and measurements of leaf increment taken at regular (ca. 5 day) intervals for the remainder of the growing season.

Flowering

Flowering and seed set data were collected from the phenological; phytosociological; and production studies. Flowering estimates were taken on population densities as low as five stems (forbs) to as high as 1000 tillers (monocots).

Belowground Plant Systems

Belowground Carex stans and C. membranacea tiller system

composition data were based on excavations of nine and four, respectively, entire tiller systems. Individual tillers were identified as being mature or immature (no dead leaves present) live tillers or dead tillers. Inter-stem rhizome distances were also recorded.

Results

Plant Growth

Average duration of the potential meadow growing season (time of 50% meadow snowmelt to 50% leaf dieback) was approximately 50 days. In 1970 it lasted for 50 days; 55 days in 1971; 45 days in 1972; and 55 days in 1973. The potential belowground growing system lagged the aboveground season by approximately two weeks. Annual variation in the initiation of the meadow growing season was on the order of 3 - 16 days.

Total tiller photosynthetic leaf increment, in both Carex stans and C. membranacea, exhibited an almost linear development until the peak of the season (Fig. 18). Post-peak season dieback was initially slow but was pronounced a week later. Earlier initiation of the growing season (1971, 1973) resulted in positive net photosynthetic leaf tissue increment ceasing at an earlier date than that when the growing season was later (1970, 1972) in its commencement. Leaf length increment occurred for only a 30 - 40 day interval of the total potential growing season (Fig. 19). Leaf increment in the youngest leaves continued on until almost the end of the potential growing season.

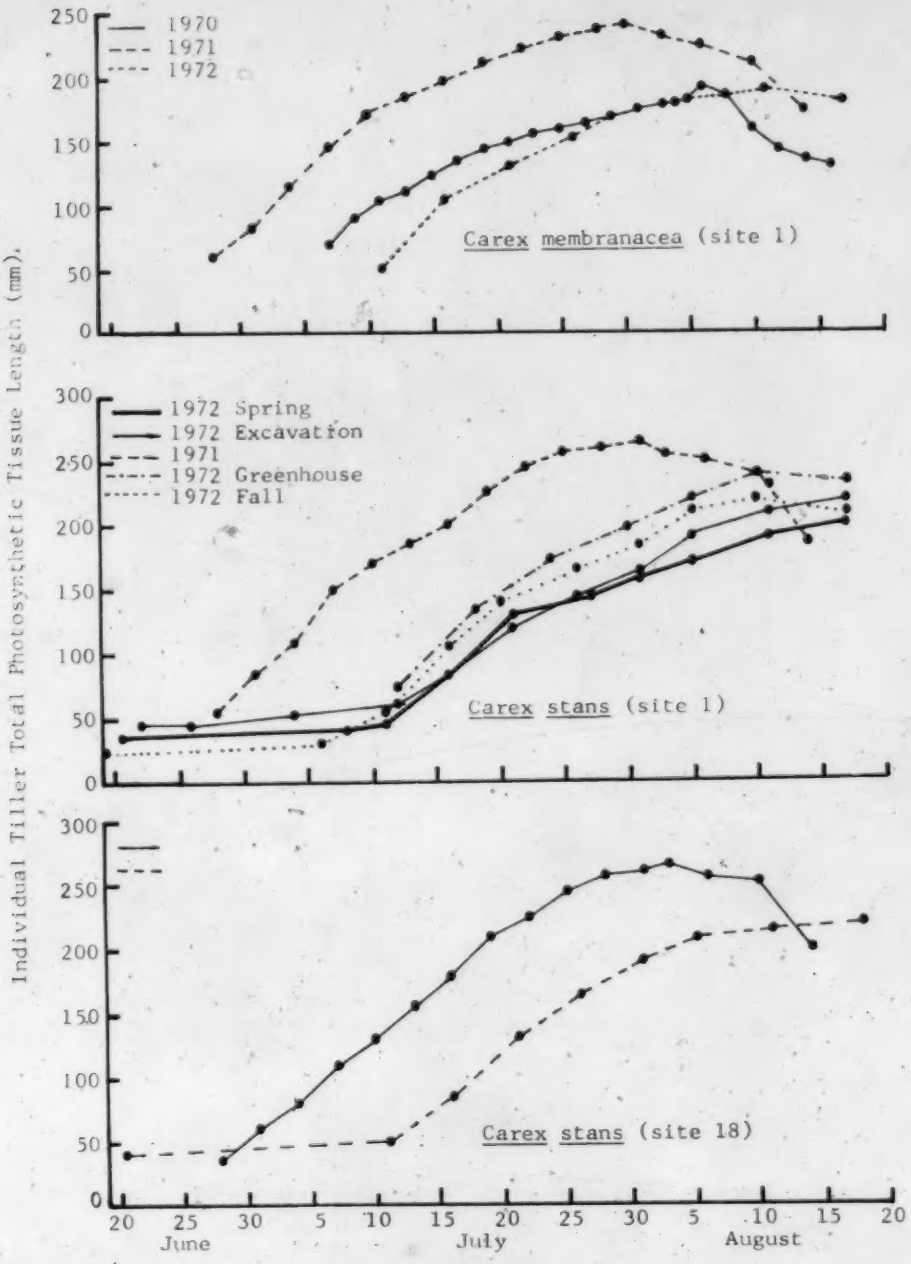

Figure 18. Seasonal Carex membranacea and C. stans individual tiller total photosynthetic leaf length increment (mm) at the hummocky intensive study (site 1) and wet (site 18) meadows 1970 - 1973.

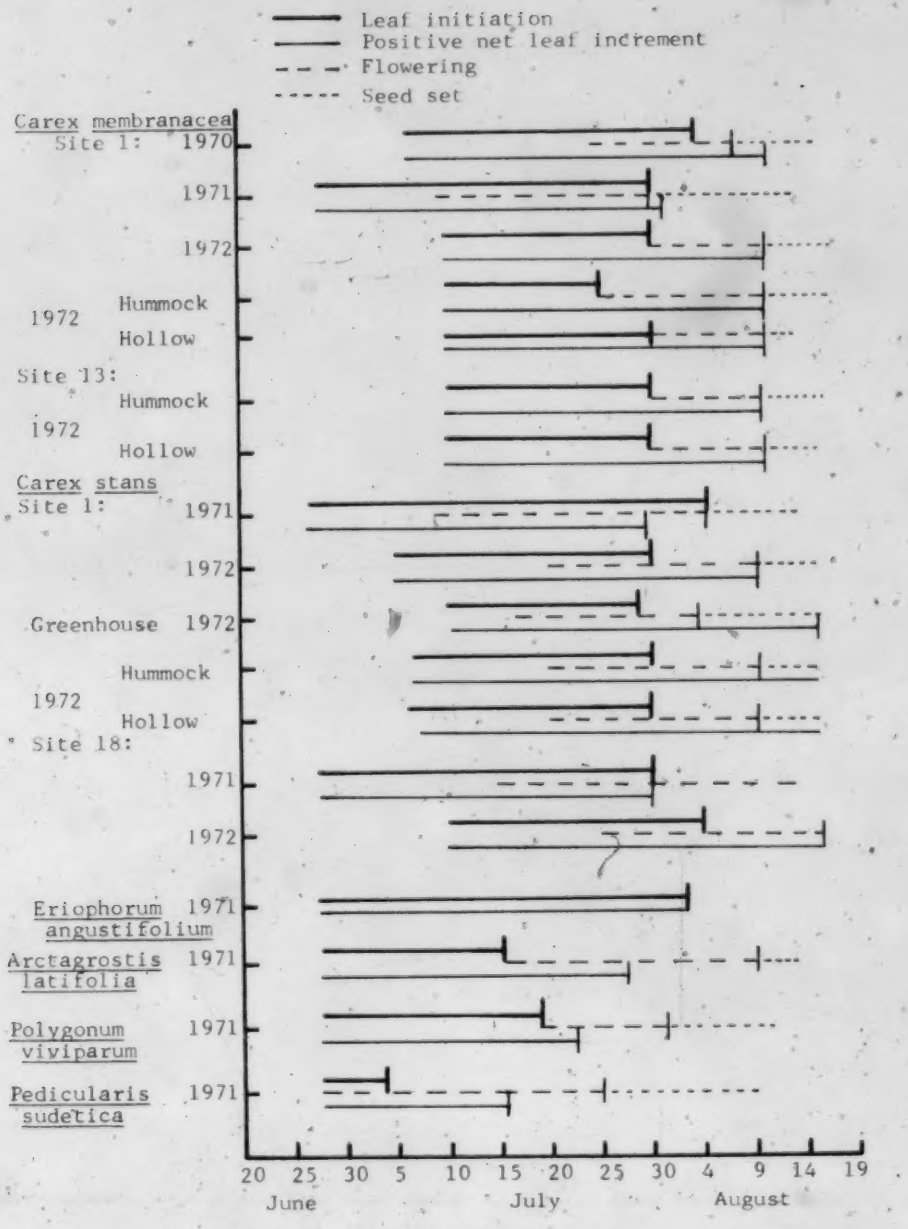

Figure 19. Phenological development of the dominant meadow species (1970 - 1972 growing seasons) in three lowland sedge-moss meadows.

In an earlier and milder season (1971) in the hummocky intensive study (site 1) meadow, total sedge tiller leaf increment was 27% greater in Carex membranacea and 18% greater in C. stans, than in a later and cooler season (1972). A similar comparison of Carex stans at the wet (site 18) meadow showed the difference to be 21%. Carex stans tillers growing (1972) in the field greenhouse had a total tiller increment 15% greater than that in controls.

Both Carex stans and C. membranacea retained over winter, 10 - 15% of their peak season photosynthetic leaf tissue in a green state (Fig. 20). Post snowmelt measurements of late fall and early-spring tagged C. stans tillers indicated a sub-snowsurface increment, in the winter green carryover tissue, of 6 - 8 mm per tiller. This represented an increment slightly less than 5% of the total seasonal leaf growth. C. stans tillers which had been prematurely excavated from the snow showed no leaf growth until immediately after natural snowmelt occurred.

Over-all inter-community variability in C. membranacea total tiller leaf increment was minimal (Fig. 21). On an intra-site hummock/hollow comparison total tiller leaf growth was almost identical, at the hummocky (site 1) meadow (Fig. 21). A similar comparison a the frost-boil (site 13) meadow showed hummock tillers to have 25% more increment than hollow tillers.

In 1971, maximum total C. stans tiller leaf lengths in wet meadow tillers were 10% greater than those of hummocky meadow tillers. In the later and cooler 1972 season, total

Figure 20. Carex stans tillers showing green tissue carried overwinter, dug up from beneath 40 cm of snow at the wet (site 18) sedge-moss meadow.

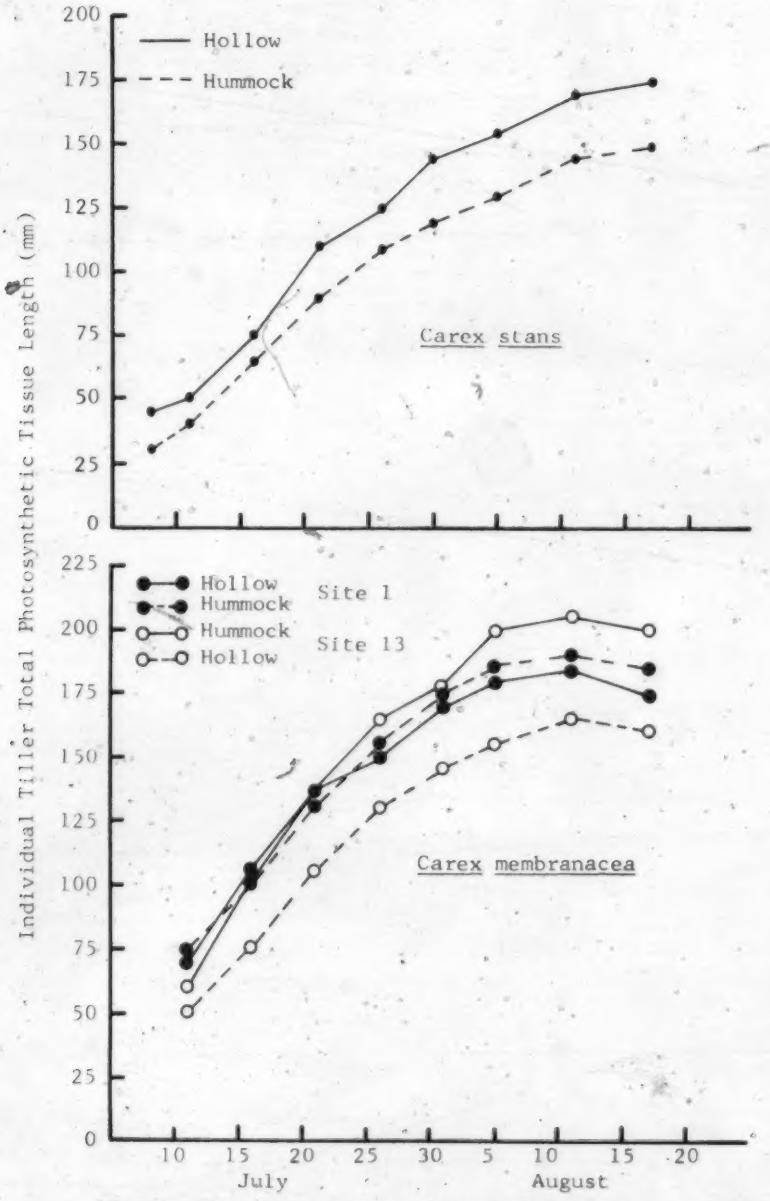

Figure 21. Individual tiller total photosynthetic leaf length increment (mm) for Carex stans and C. membranacea in hummock and hollow habitats (sites 1 and 13) 1972.

tiller leaf lengths were similar at both meadows. An intra-site (hummocky meadow) comparison of Carex stans tillers revealed hummcok inhabiting plants to have 15% more total tiller leaf length than did hollow inhabiting plants (Fig. 21). A distinctive tiller height gradient was recognizable in lowland meadow C. stans (Fig. 22). Wet meadow tillers were the tallest and frost-boil tillers the shortest. The hummcoky meadow tillers possessed an intermediate stature.

Eriophorum angustifolium and Arctagrostis latifolia developed seasonal total tiller leaf increments similar to those found in the sedges (Fig. 23). Seasonally, Eriophorum had approximately 35% of its photosynthetic tissue dominated by anthocyanin pigments.

In Pedicularis sudetica and Polygonum viviparum, maximum plant leaf growth was achieved approximately three weeks after snowmelt (initiation) (Fig. 23). Leaf growth occurred for only 24 and 18 days, respectively, of the potential growing season. Pedicularis retained its full photosynthetic leaf compliment a week longer than did Polygonum.

Salix arctica leaves expanded fully after only two weeks of growth and maintained their full photosynthetic capacity until the third week of July (Fig. 23). Leaf expansion occurred for only 12 days of the potential growing season.

Seasonal (1971) leaf growth dynamics of a representative Carex stans tiller, at the hummocky meadow, are shown

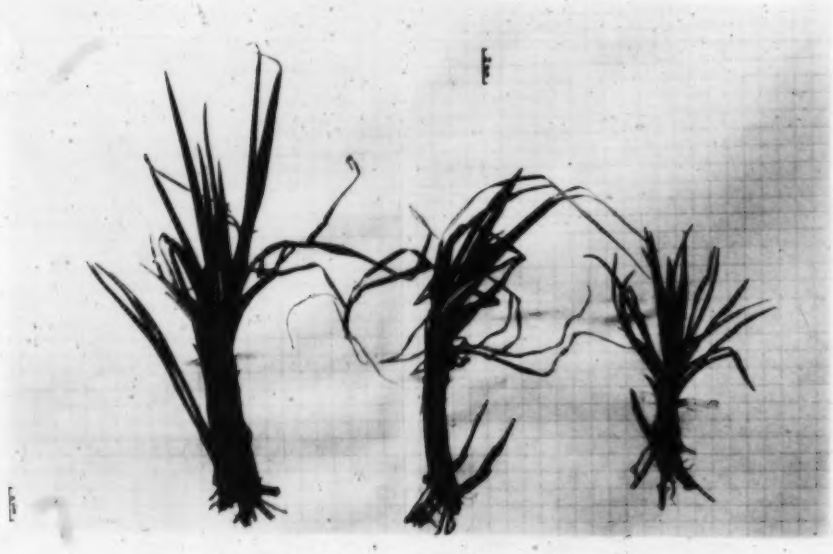

Figure 22. Carex stans tiller height gradient from a wet (left), hummocky (center), and frost-boil (right) sedge-moss meadow 1971.

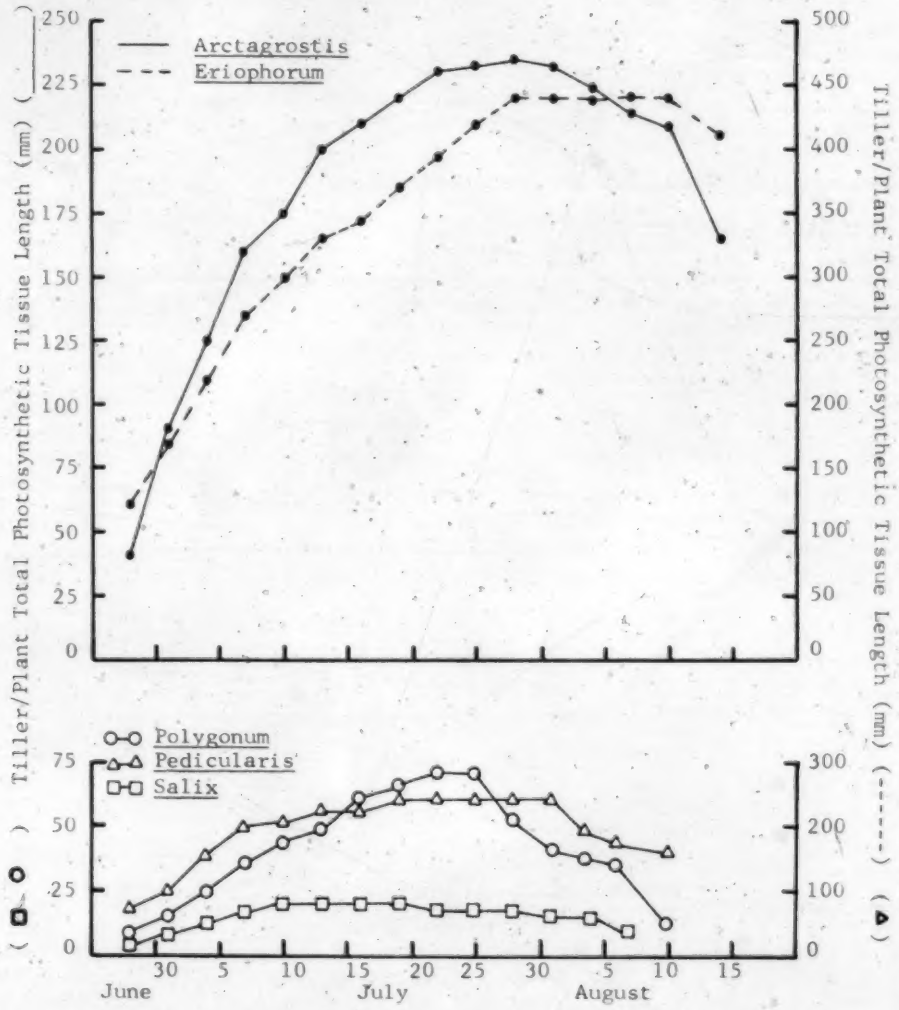

Figure 23. Individual tiller/plant total photosynthetic leaf length increment (mm) for Arctagrostis latifolia, Eriophorum angustifolium, Polygonum viviparum, and Pedicularis sudetica. Single leaf length increments (mm) for Salix arctica at the hummocky intensive study (site 1) meadow 1971.

in Fig. 24. The tiller retained three partially green leaves (A,B,C) and one fully green leaf (D) overwinter. During the growing season the two oldest leaves (A,B) showed only limited growth and had died by season's end. The two younger leaves (C,D) showed a pronounced seasonal growth and although the older (C) leaf eventually died, the other leaf (D) only died back partially. During the growing season three new leaves were formed (E,F,G). These along with the youngest leaf of the previous season (D) remained green overwinter.

The life span of a Carex stans leaf is only two years and three leaves are formed each season to replace those which die over the course of the season. Dead leaves remain attatched to the tiller for another three years. A sedge leaf becomes incorporated into the meadow litter after approximately five years from the time of its development. C. membranacea and Arctagrostis latifolia tillers showed similar leaf dynamics. Eriophorum angustifolium leaves were longer lived and were incorporated into litter after approximately seven years.

Calculations of monocot foliage pre-peak dieback (browning) and post-peak growth, as a percentage of the total seasonal growth, gave values of 1.8% at the frost-boil (site 13) meadow; 6.4% at the hummocky (site 1) meadow; and 12% at the wet (site 18) meadow. Post-peak growth accounted for slightly more than half the total amount of pre-peak dieback. Both components provided an

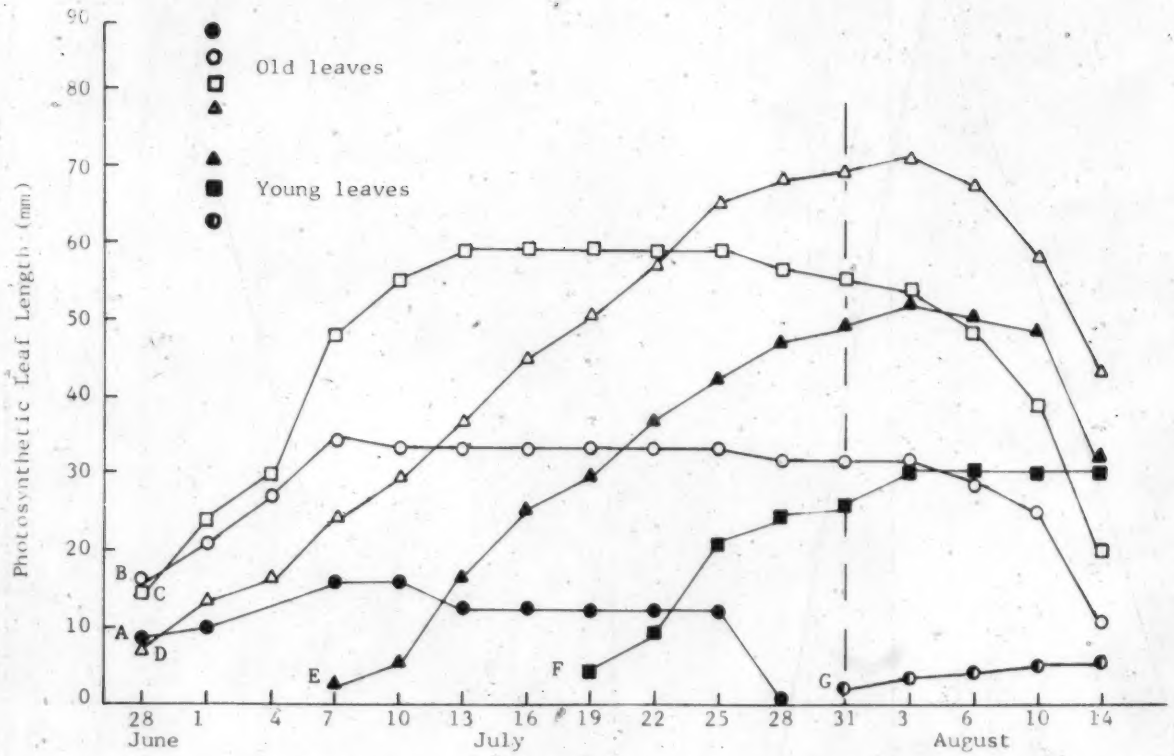

Figure 24. Seasonal leaf growth dynamics of a representative Carex stans tiller at the hummocky intensive study (site 1) meadow 1971.

important correction factor for an otherwise underestimate, using green matter only, of aboveground production. These correction factors were applied to peak season monocot shoot biomass data in calculating the total green tissue production for the year.

Flowering

Flowering rates of meadow plants were low and exhibited a distinctive annual and site variation (Table 11). Monocot species, exclusive of Luzula confusa, maintained an average population flowering rate of < 5%, with the flowering level for the forb population being < 10%. Flowering in Eriophorum triste and E. angustifolium populations were the lowest (< 2%) of all meadow monocots. Luzula confusa maintained the highest meadow flowering rates (35%). Of the forb species, Pedicularis sudetica had the highest average flowering rate (15%).

In Carex stans, the highest (8%) average flowering rates were in the wet meadow population and the lowest (4%) in the frost-boil meadow population. Arctagrostis latifolia exhibited the reverse flowering/habitat gradient. The mean total plant population flowering rates in the hummocky meadow were 110% higher than those of the frost-boil meadow and 185% higher than that of the wet meadow. Greenhouse C. stans had 14% of its population in flower, double the rate found in the controls.

In the later and cooler 1972 growing season, meadow flowering levels were 12% higher than those in an earlier

Table 11. Flowering rates (%) of various species at the frost-boil (site 13), hummocky (site 1), and wet (site 18) sedge-moss meadows 1971, 1972.

Species	Frost-boil		Hummocky		Wet	
	1971	1972	1971	1972	1971	1972
Carex stans	2.2	5.0	6.2	7.1	7.9	8.5
C. membranacea	3.5	3.9	2.8	3.9	—	—
C. misandra	5.7	8.3	2.4	6.3	—	—
Eriophorum triste	0.3	1.8	—	—	—	—
E. angustifolium	—	—	0.5	1.3	1.2	1.4
Arctagrostis latifolia	5.9	5.3	3.9	3.0	2.9	3.1
Poa arctica	—	—	—	—	2.9	2.4
Hierochloe pauciflora	3.3	1.0	8.7	10.0	1.8	1.9
Juncus biglumis	4.5	5.6	12.0	13.9	—	—
Luzula confusa	—	—	37.5	33.1	—	—
Polygonum viviparum	8.5	9.4	11.9	13.5	—	—
Saxifraga hirculus	—	—	2.6	1.3	—	—
S. foliolosa	—	—	8.5	11.9	—	—
Pedicularis sudetica	—	—	11.7	17.1	—	—
Mean	4.2	5.0	9.1	10.2	3.3	3.5

and milder season such as that in 1971. In the earlier and milder 1973 growing season, flowering levels of the frost-boil and wet meadow populations were < 0.1% and < 0.6% in the hummocky meadow populations. In the immediate area of the former greenhouse (hummcoky meadow), less than 0.8% of the plant population was flowering. This was only slightly greater than that found in non-greenhouse plants. The 1973 flowering levels were less than 4% those found in the previous two seasons. It appeared that the climatic conditions prevailing during the growing season were not expressed in the flowering rates, until the following season.

Belowground Plant Systems

Vascular species' tiller densities were 1100 stems/m^2 in the frost-boil (site 13) meadow; 1300 stems/m^2 in the wet (site 18) meadow; and 2200 stems/m^2 in the hummocky (site 1) meadow. The belowground tiller composition of Carex stans and C. membranacea are shown in Table 12.

Table 12. Mean belowground tiller system composition (number and %) of Carex stans (n=9) in hummock and hollow habitats and in combined habitats for C. membranacea (n=4) at the hummcoky intensive study (site 1) meadow 1971.

Species	Habitat	Immature tillers	Mature tillers	Dead tillers	Total plants/ system	Mean rhizome length (mm)
Carex stans	Hummock	1(7%)	6(40%)	8(53%)	15	113
	Hollow	3(14%)	5(26%)	12(60%)	20	117
	Total	4(10%)	11(33%)	20(57%)	35	115
C. membranacea	Total	5(15%)	12(37%)	16(48%)	33	105

The overall tiller system composition of both sedge species was similar. Approximately 50% of the system's tillers were dead and of the living tillers, 25% were immature in their development. In Carex stans, the portions of the system inhabiting hollows had 200% more immature tillers on their system and 50% more dead tillers. Hummock occupying portions of the system had approximately 25% fewer tillers. The majority of tillers in Carex stans (70%) and C. membranacea (65%) were clumped tillers and the remainder were spreading tillers. Clumped tillers had inter-tiller rhizome distances less than 10 mm and spreading tillers had distances up to and greater than 500 mm.

Discussion

Plant Growth

The observed 1970 - 1973 variation in the lowland meadow growing season initiation and the associated climatic conditions, were similar to those observed by Barrett (pers. comm.) in the late 1960's. Variability in late-spring and early-summer cloud cover had an equivalent effect on the incoming solar radiation and subsequently on the time of snowmelt (Courtin and Labine 1976). The potential meadow growing season ranged from 45 days in a cooler season to 55 days in a milder season. The growing season generally began by late-June (minimum) and extended through to mid-August (maximum). Although Porsild (1951) regarded the short arctic growing season as one of the major factors limiting arctic plant growth, the meadow species appeared

to be well adapted to grow under such conditions. The lowland meadow growing season was equivalent to Sørensen's (1941) proposed minimum growth period required by arctic plants. The average raised beach community growing season of 53 days was almost identical to that of the meadows (Bliss 1975). In the Low Arctic, Tieszen (1972b) reported the growing season at Barrow to be 55 days and Aleksandrova (1961) recorded it as being 60 days in depressional (meadow?) areas on Bolshoi Lakhovska Island, U.S.S.R. Savile (1972) has considered in detail the various adaptations arctic plants ahve made to such a short growing season.

The net effect of a short growing season is to be observed in the accelerated growth and development of meadow plants. Only a portion of the average 50 day potential growing season was used by the meadow plants for active leaf growth. Monocots utilized only 60 - 80% of the initial period and forbs and Salix arctica only 25 - 50% of this period. The most intensive growth period (late-June to late-July) closely coincided with high levels of incoming radiation. Early growing season radiation levels were 0.5 ly/min. and dropped to 0.2 ly/min. by the end of the active growth period (Courtin and Labine 1976). The greater (22%) 1971 sedge tiller leaf increments corresponded to somewhat higher incoming radiation levels than those found in 1972. Incoming radiation appeared to be a significant factor in regulating plant growth of meadow species but the exact mechanisms of such photoperiodic regulation were not studied.

Seasonally higher air temperatures also developed during the course of the growing season but did not show a close relationship with plant growth. Canopy air temperatures were 75% higher in 1971 than in 1972 but leaf increment was only 22% greater and production only 5% greater. The warmer, by an average 7° C, greenhouse canopy temperatures did result in increased sedge tiller: i) leaf lengths (15%); ii) leaf areas (30%); and iii) aboveground production (26%). Significant positive temperature changes such as those experienced in the greenhouses did appear to influence meadow plant growth but the mechanisms of this interaction were not studied.

Sørensen (1941,1945), Warren Wilson (1957), Svatkov (1961), and Savile (1961, 1972) considered temperature to be the critical factor in regulating arctic plant growth. Bliss (1956) found high correlations between arctic plant growth and ambient air and soil temperatures. Soil temperatures have been shown to be important in regulating alpine plant dormancy (Spomer and Salisbury 1968). Polunin (1955) and Tieszen and Bonde (1967) regarded light intensity levels as being critical to arctic plants. Although the duration of the photoperiod in the Arctic is similar to that of the alpine tundra, arctic light intensities are approximately 50% lower (Tieszen and Bonde 1967). Mayo et al. (1976) found Carex stans to be photosynthetically active (exhibit positive net assimilation) over the full 24 hr period but to have considerably lower rates during the 'night period' with

its characteristic reduced light intensity levels.

Peak leaf length increment by early to mid-August, coincided with peak shoot biomass levels. Annual growth duration of the meadow plants was 'controlled' by the time of post-snowmelt growth initiation, with growth ceasing 2 - 5 weeks before the onset of inclement weather. The relatively 'fixed' period of growth therefore shifted annually but although the 1972 growth period commenced 10 days later than in 1971, it also continued its growth for an equivalent period beyond that found in 1971. Post-peak leaf increment was less than 3% of the season's total. Tieszen (1972a) also found that meadow plants at Barrow stopped growing in advance of inclement conditions. The causes of such growth stoppage are not understood but decreasing photoperiods, lower temperatures, carbohydrate and nutrient depletions may all be implicated in this development. An internal physiological feedback mechanism (genetic?) might also be considered as a possibility. Mosquin (1966) indicated that arctic plants possessed genetic features which emphasized uniformity of character. A uniform seasonal growth pattern could be one such genetic expression. Such a conservative growth strategy would insure a greater margin of success in such an unpredictable and severe environment as found in the High Arctic.

Retention of 10 - 15% of the summer's green foliage overwinter, provided the meadow sedges with the potential for a rapid spring growth initiation. Late spring sub-snow-

surface foliage increments developed from this overwintering material. 'Ice greenhouses' formed from the interaction of high snow water levels and late spring freeze/thaw temperatures, were considered to be the sites of this growth. Although the sub-snowsurface growth was relatively minimal, it did indicate the high photosynthetic potential of the overwintering green tissue which was primarily retained in young leaves.

Sørensen (1945) found that 26% of the Greenland plants were wintergreen and that they retained overwinter leaf buds which had been formed the previous season. Savile (1972) also pointed out the extensive occurence of overwintering green tissue in arctic monocots and its importance to early spring growth. Andreev et al. (1972) found Eurasian Carex stans tillers overwintering with 23% of their green foliage but made no mention of any growth in this component. Bell (1973), working in alpine tundra, observed the development of miniature 'ice greenhouses' around Kobresia bellardii and found leaf increment occurring under such conditions. The occurence of sub-snowsurface growth in arctic plants has also been reported by Kovakina (1958) and Aleksandrova (1970b). This phenomenon is not, however, of widespread occurence and Tieszen (1972a) and Svoboda (1973) found no such growth in their low arctic meadow and lowland raised beach, respectively, communities.

Hummocks, by virtue of their warmer and better drained soil environments, increased Carex stans tiller leaf growth

by 15% over that found in hollow habitats. C. membranacea demonstrated a 25% increment in its hummock inhabiting tillers at the frost-boil meadow. The optimal nature of the hummock environment was further evident from the concentration of forbs and woody plants in this habitat. Their capacity to develop maximum photosynthetic foliage early in the season appeared to give them an advantage over hummock inhabiting monocots and minimized the latter's shading effect later on in the season.

Carex stans, C. membranacea, and Arctagrostis latifolia leaves remained attatched (live and dead) for approximately five years and then became incorporated into the litter. Eriophorum leaves remained attatched for ca. 7 years before turning over into litter. Monocot tiller life spans were estimated as being 5 - 7 years in their duration. It was not determined if the tillers belowground system (roots, rhizomes) died at the same time or if it was possibly longer lived. Such a dual natured longevity of tiller components has been reported in arctic monocots (Shaver and Billings 1975) and will be discussed in greater detail in the section on roots.

Barrow monocots initiated 3 - 4 leaves each season, with only 1 - 2 expanding and the remainder overwintering (Tieszen 1971). Sørensen (1941) estimated the life span of low arctic Carex stans tillers as being 5 - 8 years and Shaver and Billings (1975) estimated it to be 4 - 7 years for low arctic Carex aquatilis. Such relatively short life

spans for arctic sedges would create a rapid turnover of aboveground retained nutrients and additionally rejuvenate the sedge population by allowing a frequent production of new tillers. This latter development is indicated by the high (65 - 70%) incidence of tiller clumping in the lowland meadow sedges.

Flowering

Meadow plant population flowering rates were low (< 10%) and in forb species were almost double those of moncots. In the majority of species, flowering levels changed in accordance with the type of growth habitat. Flowering in the adjacent rock outcrop (dwarf shrub-heath-moss) communities was 200 - 900% higher than in the meadows but was contributed by primarily forb and woody species (Bliss and Kerik 1973). From a comparative meadow community at Barrow, 1970 flowering levels were approximately 7% of the population (Dennis and Tieszen 1972). Lowland meadow species came into flower between early July through mid-August. This flowering period is consistant with that reported for meadow species from other arctic locations (Sørensen 1941, Aleksandrova 1961, Savile 1961, Dennis and Tieszen 1972).

Vegetative reproduction, in the majority of meadow species, was more common and more successful than was floral reproduction. In the lowland meadows successful monocot seed set was never observed and the time period for its occurence was marked by extremely poor weather conditions. Based on

Sørensen's (1941) and Bliss' (1958) findings of low (< 5%) germination rates for arctic sedge seeds, a floral strategy for reproduction would appear to be impractical for meadow species. Shaver and Billings (1975) also reported that less than half of the Carex aquatilis tillers they studied, lived to flower. In the High Arctic, the meadow growing season is too short to insure that flowering will be successful and the dominant meadow flora has evolved along the lines of those capable of vegetative reproduction.

A number of environmental factors have been implicated in arctic floral reproduction. Babb (1972), Younkin (1972), and Dennis and Tieszen (1972) found that increased soil fertility in arctic meadows increased flowering rates. Sørensen (1954) indicated that increase in available nutrients stimulated greater leaf production which in turn stimulated greater flowering rates. Dennis and Tieszen (1972) have also suggested that insufficient energy reserve levels (carbohydrates?) might be limiting to floral development. Savile (1972) implicated higher air temperatures as leading to higher flowering levels and also considered the possibility that genetic factors were keeping flowering to a minimum. Considering the doubling of flowering levels in the greenhouse sedges, higher (7° C >) air temperatures did appear to stimulate flowering. A temperature/flowering relationship was further suggested by a comparison of annual flowering rates. The total degree days above zero in the earlier and warmer 1971 season were 443 and only 137 in the

later and cooler 1972 season. Corresponding flowering levels were 12% higher in 1972 but were extremely low (< 1%) in 1973. The 1973 season was comparable to the 1971 season and would have suggested considerably higher flowering rates. It would appear that any one season's flowering levels are directly proportional to the previous season's growth conditions and that temperature may play a significant role in this development. Sørensen (1941) had previously shown that low arctic Carex stans tillers initiated their floral primordia the season prior to flowering. The lower 1972 temperature regimes may have been insufficient for proper floral primordial development and limited the degree of flowering in 1973. The exact mechanisms in this relationship are not known but carbohydrate levels might be considered to play a prominent role.

Belowground Plant Systems

Meadow plant densities ranging from 1100 - 2200 stems/m^2 were comparable to the 1900 stems/m^2 reported for a sedge-cotton grass meadow in the Soviet Polar Urals (Smirnov and Tokmakova (1972). Meadow stem densities at Barrow were 120 - 335% higher than those of the lowland meadows (Dennis and Tieszen 1972). Although no quantitative data were collected, plant densities on the hummocks were ca. 100% greater than those in hollows.

In belowground sedge tiller systems, live and dead tiller distribution was almost equal. A 25% immature tiller component in these systems suggested that a tiller's life

span was on the order of 4 uears or more. The high (65 - 70%) proportion of clumped tillers suggested that a tiller's death acted as a stimulus for tiller bud formation from the base of the dying tiller. Lewis et al. (1972) have reported that the death of a Phleum alpinum tiller led to the formation of a tiller off the dying shoot. Localized concentrations of tillers would result in a greater conservation of energy and a higher efficiency in translocating such energy from the maturest (photosynthetically most active?) tillers to the less photosynthetically active immature tillers. Allessio and Tieszen (1973) found that in Dupontia fisheri, daughter tillers had more translocated carbohydrates than did the older tillers which produced them. Shaver and Billings (1975) also found that the rhizomes and roots of dead Carex aquatilis tillers lived 1 - 4 years beyond the deaths of their shoots. They continued to supply nutrients and water to the poorly rooted young clumped tillers. Environmental (hummock/hollow) influence on tillering was most obvious in the immature tillers. Hummock habitats had 20% more mature tillers but the hollows had 200% more immature tillers. This might suggest that the cooler and wetter hollow soils retarded tiller development.

MEADOW BIOMASS AND NET PRODUCTION

Prior to the initiation (1970) of the International Biological Program's Circumpolar Tundra Biome studies, data on arctic plant biomass and production were limited. The available studies (Bliss 1956, Shanks as cited by Bliss 1962a,

Dennis and Johnson 1970) were primarily from low arctic communities. Comparable Russian investigations provided community biomass data but had little to no information on production (Lavrenko et al. 1955, Aleksandrova 1958, 1970a, 1970b, Khodachek 1969).

Of the IBP Tundra Biome Studies (Heal 1971), the Devon Island program was the only representative high arctic study. Standing crop and production data for vascular plants were collected over a 2 - 4 season interval, in lowland sedge-moss meadows (reported here); in rock outcrop (dwarf shrub-heath-moss) communities(Bliss et al. 1976); and in raised beach (cushion plant) communities (Svoboda 1976).

Aboveground and belowground vascular plant standing crop and net prodcution estimates were taken at a hummocky intensive (site 1) study meadow over four (1970 - 1973) consecutive seasons and for three (1971 - 1973) consecutive seasons at a frost-boil (site 13) and wet (site 18) meadow. In 1971, three extensive hummocky (sites 4,7,10) meadow stands were studied for biomass content and production. Seasonal leaf length increment data provided a correction factor for pre-peak season dieback and post-peak season growth and allowed for a refinement of seasonal production estimates.

Different interpretations of basic terminology can often lead to inaccurate comparisons or misinterpretations of biomass and production data. To minimize this, the more common terms used in the following sections have been

defined as follows:

1. Aboveground biomass/standing crop: the total weight of both living and dead attatched vascular plant parts (excluding plant roots and rhizomes) in the identifiable moss layer overlying the more humified organic soil.

2. Belowground biomass/standing crop: the weight of all vascular plant rhizomes and roots found within the dead moss and soil.

3. Biomass or standing crop: used interchangeably to define total (live and dead) vascular plant weight from a defined unit area of the community at a particular time of the year.

4. Harvest: the physical removal by clipping, of all vascular plant material from a defined unit area of meadow at a particular time in the growing season.

5. Net production: the measureable portion of gross production not transpired or translocated and available for consumption.

6. Primary production: the measured increase in vascular plant biomass/standing crop over a period of time, inclusive of any losses sustained during this interval.

7. Productivity: the rate of vascular plant production per unit time of the growing season.

8. Sod: tight mat of easily separated moss material, vascular plant stem bases, rhizomes, and roots, lying close to the surface but above or on the soil proper.

Methods

Aboveground

Estimates of meadow vascular plant standing crops and production were based on the harvest method (Milner and Hughes 1970). The studies were conducted over 1 - 4 seasons (1970 - 1973) and involved from 1 - 6 different meadows (Table 13). Sestak and Jarvis (1971) found the harvest method, compared to other available methods, the best for following growth and production rates in natural vegetation. Sample size of harvested material was 20 X 20 cm in 1970 and 20 X 50 cm in all other years.

Harvesting at the hummocky intensive study (site 1) meadow (Fig. 25) was carried out in randomly selected and seasonally retained 5 X 5 meter plots. The outermost two peripheral rows of staked plots were used for such destructive sampling and the central unstaked portion of the meadow was used as a control. In the extensive meadow stands randomly located samples (3/plot) were harvested in a pair of staked 4 X 8 meter plots.

For each sample harvested, all vascular plant material above the moss surface was clipped and collected. Stem base, rhizome, and root biomass data were obtained from triplicate 20 X 20 cm sod block (10 cm depth) collected on each harvest date in conjunction with aboveground sampling. All the collected biomass was sorted by species into its morphological components (Fig. 26). The sorted material was oven dried (85° C for 24 hr) prior to being weighed (0.1 gram

Table 13. Lowland sedge-moss meadow stands sampled (harvest and sample number) for seasonal aboveground and belowground primary production 1970 - 1973.

Meadow	Site	Season	Aboveground Harvest	Aboveground Samples	Belowground Harvest	Belowground Samples
Hummocky	1*	1970	5	16	5	16
		1971	6	10	5	3
		1972	6	10	6	6
		1973**	1	10	3	6
Hummocky	4	1971	4	6	4	3
Hummocky	7	1971	4	6	4	3
Hummocky	10	1971	4	6	4	3
Frost-boil	13	1971	5	6	5	3
		1972	4	6	5	6
		1973**	1	6	1	3
Wet	18	1971	5	6	5	3
		1972	4	6	5	1
		1973**	1	6	1	3

* intensive study meadow.

** harvest taken at time corresponding to peak season - August 9.

Figure 25. The hummocky intensive study (site 1) meadow studied as a representative lowland meadow stand by all disciplines. Meteorological station in background.

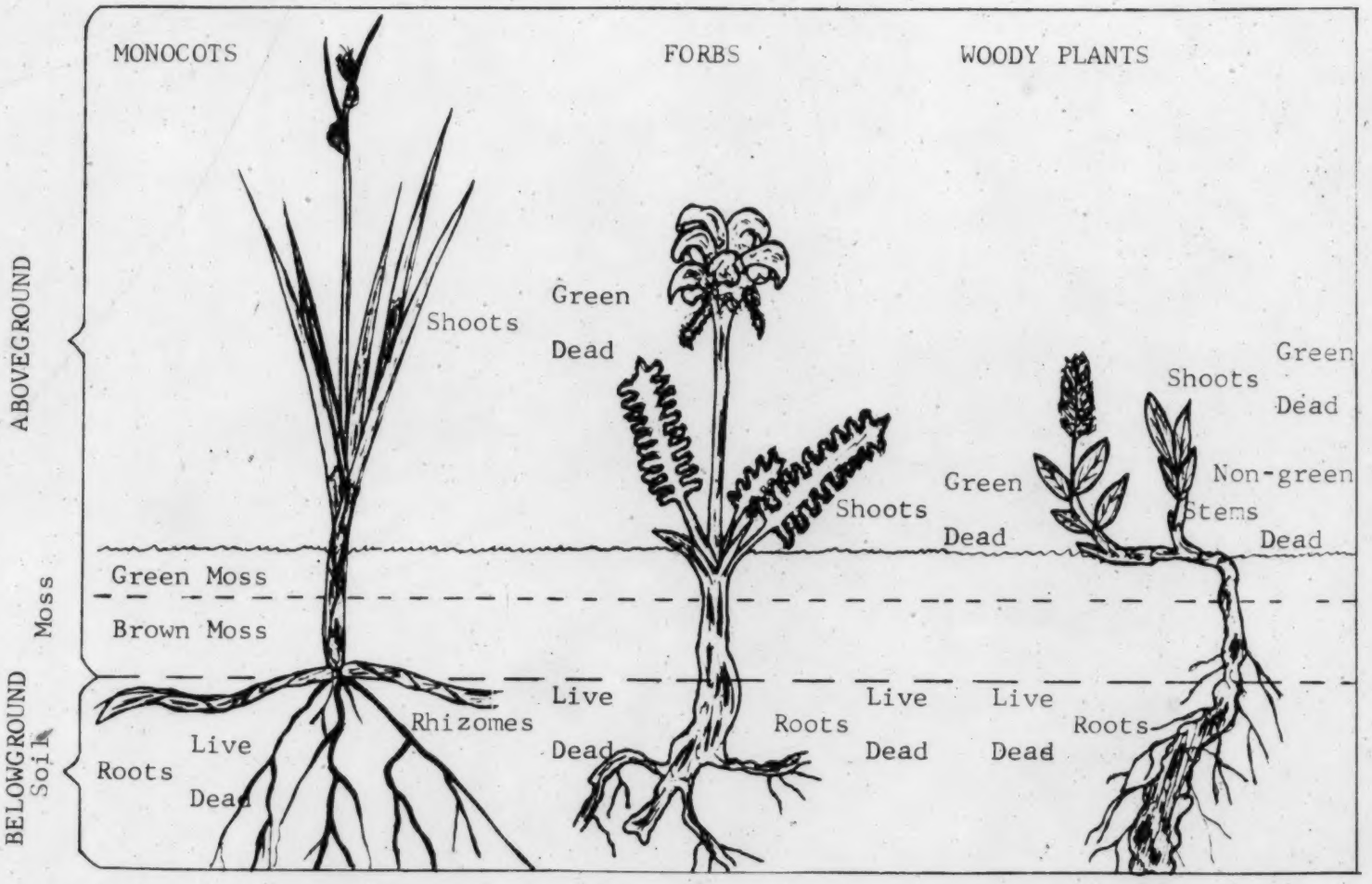

Figure 26. Morphological units and their divisions, used in sorting the sedge-moss meadow vascular plant biomass for production studies.

accuracy. Greenhouse biomass and production studies were restricted to the aboveground component and were based on a single harvest (August 18, 1972) consisting of duplicate 20 X 20 cm samples from each of the two field greenhouses.

Monocot pre-peak season dieback and post-peak season growth estimates were based on leaf increment data. These calculations were used to 'adjust' the monocot peak season aboveground green biomass data. No such correction factors were necessary for forb or woody species.

Belowground

Estimates of belowground vascular root and rhizome standing crops and production were also based on the harvest method. Sampling extended for 1 - 4 consecutive seasons (Table 13) and the root biomass and production estimates based on either sod block (1971) or core (1970, 1972, 1973) samples. In 1970, core samples (6 cm diameter) were taken in conjunction with aboveground sampling. In 1972 and 1973, the core samples were collected from a 4 X 8 meter staked plot outside the aboveground sampling plots. The above sampling, done on a weekly basis, was not synchronous with the aboveground sampling but coincided closely for the major harvesting dates. In 1971, the sod block samples (n=3) were collected at the time of the aboveground sampling. All root cores were taken to the depth of thaw but the sod blocks were only collected to a depth of 10 cm, a depth which included the vascular plant stem bases, rhizomes, and a portion of the rooting biomass. In 1972,

and 1973, root cores were separately collected from hummock and hollow habitats at the intensive hummocky study (site 1) meadow and the frost-boil (site 13) meadow.

Monocot roots and rhizomes as well as forb and woody plant roots were easily removed from the sod block samples. Root cores were handled in a similar way. The remaining material from both of these samples was then washed in water to collect the finer roots and the wash water further screened (4 mm mesh)to insure maximum collection of root material. For the August (1973) root core samples, each 25 cm core was carefully divided into 5 cm segments and the roots collected as above.

Subsamples ($\leq$ 0.1 g oven dry weight) of washed roots were taken from each of the 1972 and 1973 root cores for live:dead root analyses. Each subsample was visually sorted into live (turgid, white/tan) and dead (flaccid, brown/black) components as had been done by Dennis (1968). Verification of the method's accuracy was undertaken by means of a histochemical tetrazolium chloride salt viability test (Jensen 1962). Sorted live and dead roots were immersed for a 24 hr period in a solution of equal parts: 0.1 M phosphate buffer (pH 7.4); 0.1 M sodium succinate; and 1 mg/l solution of tetrazolium chloride. Pink coloration of the root's vascular tissue (high metabolic activity), revealed under a stereo microscope, indicated a viable (live) root condition.

An 'in situ' study of Carex stans tiller root growth

was carried out in 1971 at the hummocky intensive study (site 1) meadow. Twenty sedge tillers were excavated along with their frozen soil on July 4. The plants were thawed out in the laboratory; removed from the soil and their attatched roots identified (drawings) and measured; the roots covered (marked) with powdered charcoal; and the tillers transplanted in plastic perforated pots back in the original excavation pits. The tillers were re-excavated at the estimated peak of the aboveground growing season (August 14) and the roots (original, elongated, and new) measured; clipped and sorted as to origin; and oven-dried at 85° C for 24 hr prior to weighing.

Aboveground Production Estimates

The relatively homogeneous meadow plant cover, unlike that of raised beach and rock outcrop communities, permitted calculation of aboveground production on the basis of difference measurements of green and non-green tissues. Net production was calculated separately for each plant group - monocots, forbs, and woody plants. Peak green monocot biomass was quantitatively increased by correcting for pre-peak season dieback and post-peak season growth. This was equivalent to increments of 1.8% in the frost-boil (site 13) meadow biomass; 6.4% in the hummocky (site 1) meadow biomass; and 12% in the wet (site 18) meadow biomass. Inter-seasonal variation in this correction factor was less than 6%. No biomass corrections were found to be necessary for forbs or woody plants. The 1973 single peak season harvest data were

used to calculate production on a comparative biomass: production ratio basis with the 1971 biomass data. Both the 1971 and 1973 growing seasons were similar and net production, based on the available standing crop, was also considered to be similar.

Belowground Production Estimates

Monocot rhizomes as well as forb and woody plant roots were concentrated in the upper 5 cm of the soil/moss layer and were readily collected from the sod block samples. Net production estimates of these plant components were based on difference measurements of their total (live and dead) biomass.

Monocot root production was considerably more difficult to estimate because of the deeper distribution ($>$ 25 cm) of the roots and the continued thawing of the soil over the growing season. Total root collections were made from the cores taken at each harvest but their different depths did not allow calculation of production based on weight differences. A statistical approach to calculating root production was used in order to get around this difficulty.

A linear regression was carried out on the 'soundest' seasonal total belowground biomass data. The July 22 through to August 22 (1972) belowground data for the hummocky intensive study (site 1) meadow were used because they were collected on a weekly basis; a relatively uniform (18 - 23 cm) thaw depth prevailed over the sampling period; and an estimate of the vertical root distribution in the meadow was

available. All sample data used were extended or reduced to a uniform 20 cm depth from extrapolations based on the vertical root distribution pattern. All calculations were made on a separate basis for hummock and hollow habitats and total meadow production based on the meadow area coverage by each specific habitat.

Computed seasonal monocot net root production (80% confidence limits) was 5.10±6.03% of the initial total root standing crop. Belowground production beneath the hummocks was 5.3±6.0% ($y=6.557 + 0.011x$) and 4.8±6.32% ($y=3.387 + 0.005x$) beneath the hollows.

An aboveground (green + non-green):belowground monocot net production ratio of 1:2.73 was calculated for the hummcoky intensive study (site 1) meadow. This ratio was used in estimating monocot root production in other sedge-moss meadows from which biomass data were available. The overall similarity of inter-meadow plant growth suggested that this was the most accurate and practical approach to use. Total belowground prodcution was on monocot root and rhizome production plus forb and woody plant root production.

The statistically calculated belowground monocot root production which formed a large portion of the total root production, was potentially an underestimate. It did not take into account pre- and post-sampling period growth nor did it account for root growth below the sampled depths. These two factors were not considered to alter the production estimates significantly since the low soil temperatures early

and late in the season were not considered to be conducive to any substantial amount of root growth.

Results

Aboveground

In each of the production sampled meadow stands, with the exception of the wet (site 18) meadow, monocots made up approximately 85% of the biomass; woody plants 10%; and forbs the remaining 5%. In the wet meadow, monocots provided approximately 95% of the total biomass and forbs the remaining 5%. The short growing season, averaging 50 days, made peak biomass development times occur relatively synchronously in all three plant groups. In limited situations where there was suggestion of asynchronous development peaks, forb and woody plant biomass peaks were only a week or so earlier than those in monocots. Average early (late June - early July); mid (late July); and late (early - mid-August) season standing crops for each major meadow type are shown in Figure 27.

1. Live biomass.

Seasonal increment in the green biomass showed a linear development in all the meadow stands sampled and peak biomass levels occurred by early (mild season) to mid-(cool season) August. The lowest average early-season green biomass content was found in the wet (site 18) meadow (7 g/m^2) and the highest was found in the hummocky meadows (12 g/m^2). The higher levels in the hummocky meadows was primarily the result of earlier growth initiation in the plateau-base hummocky (site 10) meadow. Pre-snowmelt lowland meadow green biomass content

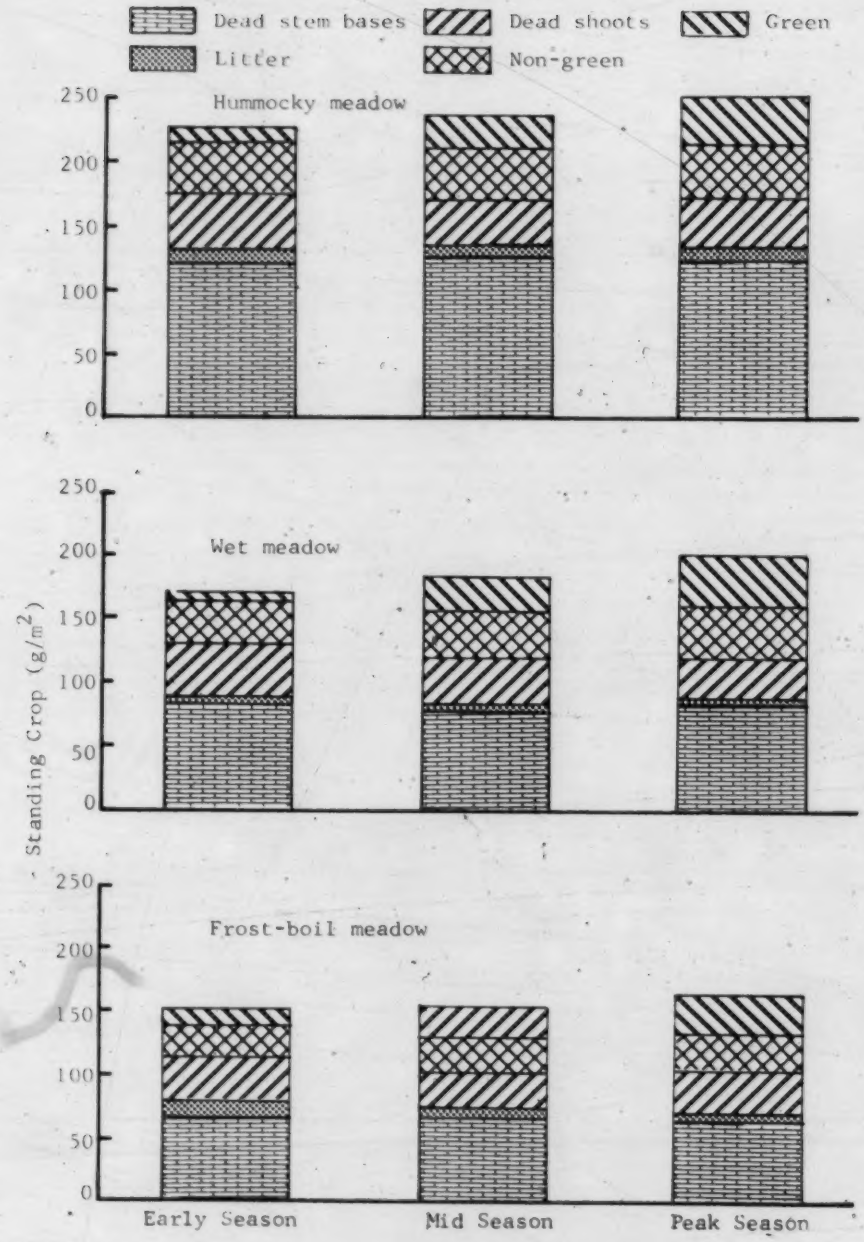

Figure 27. Aboveground standing crops (g/m^2) in early (late June-early July); mid (late July - early August); and peak (early - mid August) season at the hummocky (site 1), frost-boil (site 13), and wet (site 18) meadows (2 - 4 yrs data).

averaged 5.9 g/m^2 and ranged from 4.3 - 7.9 g/m^2. Monocots contributed 85% of the total and forbs the remaining 15%. Under a light snowcover in early September, green tissue content of the meadow standing crop was 8.5 g/m^2 at the hummocky intensive study (site 1) meadow. This was roughly 25% of the peak season green biomass content and still 45% greater than that found prior to snowmelt.

Non-green tissue increment was less pronounced in its development and in the frost-boil (site 13) and hummocky (sites 4,7,10) meadows actually showed a mid-season drop. Early season green:non-green tissue ratios ranged from a low of 1:2.2 in the frost-boil (site 13) and extensive hummocky (sites 4,7,10) meadows to a high of 1:4.6 in the hummocky intensive study (site 1) and wet (site 18) meadow. By the peak of the season, these ratios had dropped considerably and the maximum level of 1:1.4 was found in the hummocky intensive study (site 1) meadow. In all the meadows sampled season to season variability in peak live aboveground biomass was slightly less than 10% (Table 14).

2. Dead biomass.

At the beginning of the growing season litter averaged 26% of the total aboveground (moss surface) dead vascular plant standing crop. By season's end its contribution had dropped to an average of 14%. Peak meadow litter levels were found immediately after snowmelt and were considerably lower (54%) by season's end. The highest average meadow litter content was measured at the intensive study (site 1) meadow

Table 14. Seasonal peak aboveground and belowground live, dead (litter included) and total vascular plant standing crops (g/m^2) and ratios in a frost-boil (site 13), hummocky (site 1), and wet (site 18) sedge-moss meadow 1970 - 1973.

Meadow	Year												
ABOVEGROUND	Live	Dead	Total	Live	Dead	Total	Live	Dead	Total	Live	Dead	Total	Mean
Frost-boil	___	___	___	55	106	161	57	121	178	59	112	171	170
Hummocky	80	211	291	91	194	285	87	193	280	84	191	275	283
Wet	___	___	___	79	132	211	76	120	196	84	121	205	204
BELOWGROUND													
Frost-boil	___	___	___	336	298	634	370	329	699	331	290	621	651
Hummocky	997	848	1845	1073	947	2020	1186	1019	2205	1110	950	2066	2034
Wet	___	___	___	698	610	1308	683	599	1282	801	710	1511	1367
TOTAL													
Frost-boil	___	___	___	391	404	795	427	450	877	390	402	792	821
Hummocky	1077	1059	2136	1164	1141	2305	1273	1212	2485	1194	1147	2341	2317
Wet	___	___	___	777	742	1519	759	719	1478	885	831	1716	1571
RATIOS (ABOVE:BELOW)													
Frost-boil	___	___	___	6.1	2.8	3.9	6.5	2.7	3.9	5.6	2.6	3.6	3.8
Hummocky	12.5	4.0	6.3	11.8	4.9	7.1	13.6	5.3	7.9	13.2	5.0	7.5	7.2
Wet	___	___	___	8.8	4.6	6.2	9.0	5.0	6.5	9.5	5.9	7.4	6.7

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with a litter content of 12 g/m^2 and the lowest in the wet (site 18) meadow with 6 g/m^2. The frost-boil (site 13) meadow with only half of its surface area heavily vegetated had a surprisingly high litter content of 11 g/m^2.

Attatched aboveground dead shoot biomass showed a weight decline over a portion or the entire interval of the growing season. The wet meadow possessed the highest (40 g/m^2) early season dead shoot standing crop and the frost-boil meadow the lowest (33 g/m^2). At the end of the season the highest (42 g/m^2) standing crops were in the hummocky intensive study meadow and the lowest (31 g/m^2) in the extensive hummocky (sites 4,7,10) meadows. By early September these had increased by another 40% at the hummocky intensive study meadow.

Moss retained dead stem base material of vascular plants, was 20 - 160% greater than the total aboveground (litter and dead shoots) dead standing crop in the early part of the season and increased to 55 - 270% by the peak of the season. In all the meadow stands, with the exception of the frost-boil meadow, dead stem base tissue levels increased slightly. Stem base material was still 'technically' considered to be aboveground biomass and was added to the dead shoot and litter standing crops to calculate the total aboveground dead standing crop. It ranged from an average high of 197 g/m^2 at the hummocky intensive study meadow to a low of 113 g/m^2 at the frost-boil meadow. Annual variation in this aboveground component was less

than 15%.

3. Lowland meadow biomass.

On a seasonal (1971) comparison (Fig. 28) the hummocky intensive study (site 1) meadow maintained the highest non-green (55 g/m^2); dead stem base (144 g/m^2); dead shoot (35 g/m^2); and litter (12 g/m^2) standing crops. The plateau-base hummocky (site 10) meadow contained the highest green tissue biomass (50 g/m^2) but also possessed the lowest non-green (24 g/m^2); dead stem base (60 g/m^2); and dead shoot (28 g/m^2) biomass levels. The lowest green tissue levels were found in the frost-boil (site 13) meadow (29 g/m^2) and the lowest litter levels in the wet (site 18) meadow (6 g/m^2). Early season total aboveground standing crop was highest in the hummocky intensive study meadow (275 g/m^2) and was lowest in the frost-boil meadow (151 g/m^2). Corresponding peak season standing crops were 285 and 162 g/m^2, respectively. Standing crop differences between the lowland hummocky meadows (sites 1,4,7,10) were less than 10%. On a comparative meadow community type basis, hummocky meadow standing crops were 10 - 80% greater than those of the frost-boil meadow and 15 - 30% greater than those of the wet meadow. The wet meadow had a 35% higher biomass content than did the frost-boil meadow. Similar early season live: dead ratios (1:3.3 average) were found in all the meadows but had dropped to an average of 1:1.9 by peak season.

4. Net production.

Average seasonal aboveground net production and net

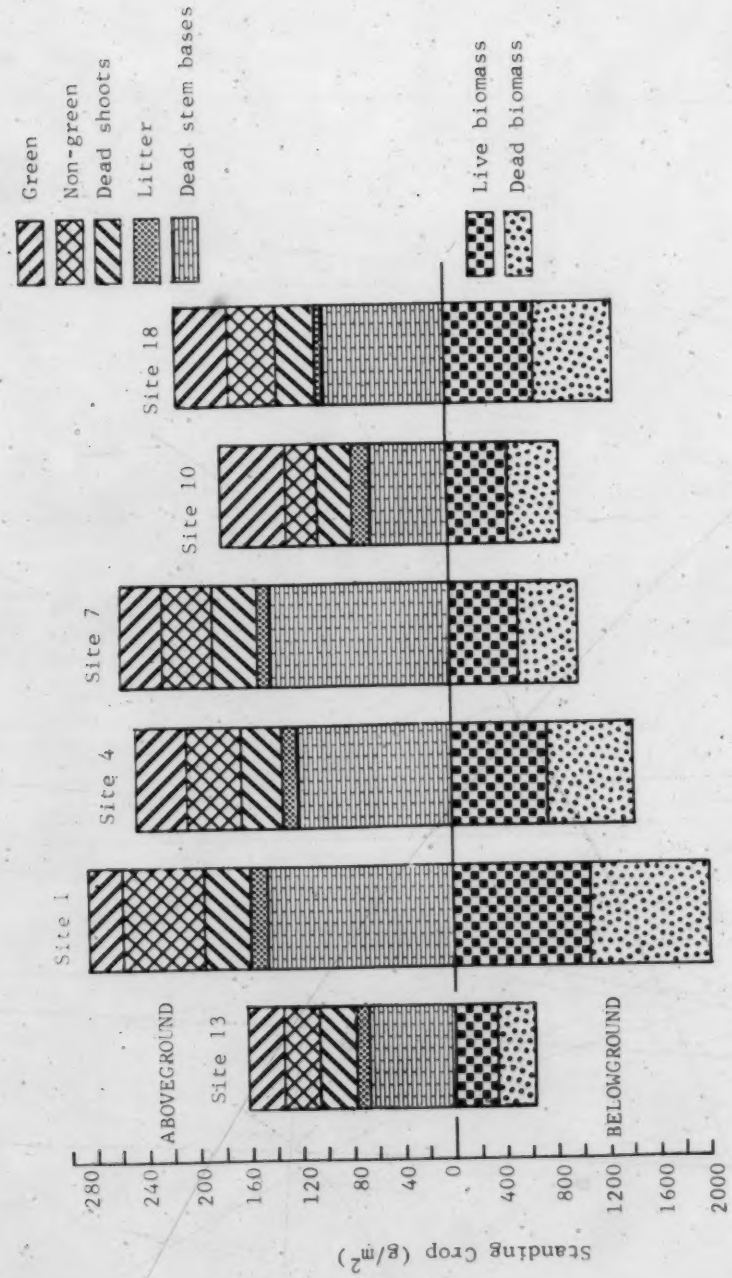

Figure 28. Peak season aboveground and belowground standing crops (g/m^2) in a frost-boil (site 13); hummocky (sites 1,4,7,10); and wet (site 18) sedge-moss meadow 1971.

productivity of the three meadow community types is presented in Table 15. The actual seasonal (1970 - 1973) data for each meadow sampled is presented in Tables 16, 17, 18, and 19.

In the frost-boil meadow (site 13) 70% of the aboveground production was by monocots; 25% by woody plants; and 5% by forbs. Corresponding contributions in the hummocky meadows were 70; 20; and 10%, respectively. In the wet (site 18) meadow over 95% of the production was by monocots and the remaining 5% by forbs. In the frost-boil (site 13) and hummocky intensive study (site 1) meadow over ca. 75% of the total aboveground production was in green plant material with a corresponding 85% in the wet (site 18) meadow. Meadow production peaked by early to mid-August.

The wet meadow was the most productive (45 ± 0.5 g/m^2) lowland meadow and the frost-boil (site 13) meadow the least productive (28 ± 1.4 g/m^2). Production in the hummocky intensive study meadow ranged from a low of 42 g/m^2 in 1970 to a high of 47 g/m^2 in 1972. Corresponding maxima at the frost-boil and wet meadow were 30 and 46 g/m^2, respectively, and minima were 25 and 45 g/m^2, respectively.

Production (1971) in the hummocky intensive study (site 1) meadow was approximately 25% higher than in the extensive hummocky (site 4,7,10) meadows. The coastal hummocky (site 7) meadow had an annual production (30 g/m^2) which was 30 - 35% less than that found in any of the other hummocky meadows (Fig. 29). The wet meadow had the highest green

Table 15. Average net primary production (g/m^2 ±standard error) and productivity* ($g/m^2/day$ ± standard error) for vascular plants in a frost-boil (site 13), hummocky intensive study (site 1), average hummocky (sites 1,4,7,10), and wet (site 18) sedge-moss meadow (based on 1 - 4 years data). A calculation is also made for a representative** lowland sedge-moss meadow.

Plant Group	Component	Sedge-moss Meadow				
		Frost-boil	Intensive Study Meadow	Average Hummocky	Wet	Representative Lowland Meadow
Monocots	Green	15.8±0.6	23.3±0.3	23.1±1.6	37.7±0.6	20.6
	Non-green	3.3±0.3	9.0±1.0	7.0±1.4	6.3±0.3	5.3
	Rhizomes	2.8±0.4	8.5±0.6	7.2±0.9	7.5±0.9	5.2
	Roots***	52.2±2.4	88.1±2.4	82.6±5.4	120.5±6.5	70.8
Forbs	Green	1.3±0.3	4.6±0.4	3.6±0.6	1.4±0.2	2.5
	Roots	0.5±0.1	1.2±0.1	1.2±0.2	1.0±0.2	0.9
Woody Plants	Green	4.5±1.7	5.1±0.2	5.3±0.6	_____	4.7
	Non-green	2.8±0.3	2.3±0.7	2.5±0.5	_____	2.5
	Roots	3.3±0.6	5.1±0.7	5.5±0.6	_____	4.2
TOTAL	Net aboveground production	27.7±1.4	44.2±1.1	41.7±2.0	45.4±0.5	35.6
	Net belowground production	58.9±2.3	102.9±2.4	96.5±5.6	128.7±1.0	81.1
	Total production	86.6±3.4	147.1±3.4	138.2±7.6	174.1±8.8	116.7
	Above:Below	1:2.1	1:2.4	1:2.3	1:2.8	1:2.3
	Aboveground primary productivity	0.54±0.1	0.87±0.1	0.79±0.1	0.88±0.1	0.68
	Belowground primary productivity	1.16±0.1	2.02±0.1	1.84±0.1	2.51±0.2	1.57
	Net primary productivity	1.70±0.2	2.89±0.2	2.63±0.2	3.39±0.2	2.25

* based on growing seasons of: 50 days-1970, 55-1971, 45-1972, 55-1973.
** based on lowland area occupied by each meadow type (hummocky-50%, frost-boil-45%, wet-5%).
*** based on sampling depth of 20 cm from the moss surface.

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Table 16. Average vascular plant net primary production (g/m^2 ±standard error) and seasonal* primary productivity, (g/m^2/day±standard error) at the hummocky intensive study (site 1) sedge-moss meadow 1970 - 1973.

Plant Group	Component	Growing season 1970	1971	1972	1973	Average
Monocots	Green	23.1	23.3	22.9	23.8	23.3±0.3
	Non-green	7.1	10.2	11.0	7.7	9.0±1.0
	Rhizomes	7.1	8.7	10.1	8.2	8.5±0.6
	Roots**	82.4	91.5	92.6	86.0	88.1±2.4
Forbs	Green	3.3	5.6	4.5	4.8	4.6±0.4
	Roots	1.0	1.3	1.2	1.1	1.2±0.1
Woody Plants	Green	4.7	5.6	5.4	4.8	5.1±0.2
	Non-green	4.1	2.3	0.9	1.7	2.3±0.7
	Roots	6.6	5.3	3.1	5.4	5.1±0.7
TOTAL	Net aboveground production	42.3	47.0	44.7	42.8	44.2±1.1
	Net belowground production	97.1	106.8	107.0	100.7	102.9±2.4
	Total net production	139.4	153.8	151.7	143.5	147.1±3.4
	Ratio above:below	1:2.3	1:2.3	1:2.4	1:2.4	1:2.4
	Aboveground primary productivity	0.85	0.85	0.99	0.78	0.87±0.1
	Belowground primary productivity	1.94	1.94	2.38	1.83	2.02±0.1
	Net primary productivity	2.79	2.79	3.37	2.61	2.89±0.2

* based on growing seasons of: 50 days-1970, 55-1971, 45-1972, 55-1973.

** based on sampling depth of 20 cm from the moss surface.

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Table 17. Average vascular plant net primary production (g/m^2±standard error) and seasonal* primary productivity (g/m^2/day±standard error) at three extensive lowland hummocky (sites 4,7,10) sedge-moss meadows 1971.

Plant Group	Component	Sedge-moss Meadow Site 4	Site 7	Site 10	Average
Monocots	Green	22.7	16.3	30.8	23.3±4.0
	Non-green	8.6	2.4	1.9	4.3±2.2
	Rhizomes	8.2	3.8	4.2	5.4±1.4
	Roots**	85.4	51.1	89.3	75.3±12.2
Forbs	Green	2.7	0.6	3.4	2.2±0.8
	Roots	2.2	0.9	1.0	1.4±0.4
Woody Plants	Green	4.1	8.8	3.8	5.6±1.6
	Non-green	4.2	1.9	2.2	2.8±0.7
	Roots	5.4	8.3	4.1	5.9±1.2
TOTAL	Net aboveground production	42.3	30.0	42.1	38.1±4.1
	Net belowground production	101.2	64.1	98.6	87.9±12.0
	Total net production	143.5	94.1	140.7	126.1±16.0
	Ratio above:below	1:2.4	1:2.1	1:2.3	1:2.2
	Aboveground primary productivity	0.77	0.55	0.77	0.70±0.1
	Belowground primary productivity	1.84	1.17	1.79	1.60±0.2
	Net primary productivity	2.61	1.72	2.56	2.30±0.3

* based on growing seasons of: 50 days-1970, 55-1971, 45-1972, 55-1973.

** based on sampling depth of 20 cm from the moss surface.

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Table 18. Average vascular plant net primary production (g/m^2 ± standard error) and seasonal primary productivity (g/m^2/day ± standard error) at the frost-boil (site 13) sedge-moss meadow 1971 - 1973.

Plant Group	Component	Growing Season 1971		1972		1973		Average	
		**Actual	Total	Actual	Total	Actual	Total	Actual	Total
Monocots	Green	14.8	29.0	16.7	32.7	16.0	31.3	15.8±0.6	31.0±1.1
	Non-green	2.7	5.3	3.9	7.6	3.3	6.5	3.3±0.3	6.5±0.7
	Rhizomes	2.5	4.9	3.7	7.3	2.3	4.5	2.8±0.4	5.6±0.9
	Roots***	47.8	93.7	56.2	110.2	52.7	103.3	52.2±2.4	102.4±4.8
Forbs	Green	1.6	3.1	1.6	3.1	0.6	1.2	1.3±0.3	2.5±0.6
	Roots	0.6	1.2	0.5	1.0	0.5	1.0	0.5±0.1	1.1±0.1
Woody Plants	Green	5.2	10.2	5.7	11.2	2.6	5.1	4.5±1.7	8.8±1.9
	Non-green	3.1	6.1	2.3	4.5	2.9	5.7	2.8±0.3	5.5±0.5
	Roots	4.5	8.8	2.8	5.5	2.6	5.1	3.3±0.6	6.5±1.2
TOTAL	Net aboveground production	27.4	53.7	30.2	59.2	25.4	49.8	27.7±1.4	54.3±2.7
	Net belowground production	55.4	108.6	63.2	123.9	58.1	113.9	58.9±2.3	115.5±4.5
	Total net production	82.8	162.4	93.4	183.1	83.5	163.7	86.6±3.4	169.7±6.7
	Ratio above:below	1:2.0	1:2.0	1:2.1	1:2.1	1:2.3	1:2.3	1:2.1	1:2.1
	Aboveground primary productivity	0.50	0.98	0.67	1.31	0.46	0.90	0.54±0.1	1.06±0.1
	Belowground primary productivity	1.01	1.98	1.40	2.75	1.06	2.08	1.16±0.1	2.27±0.2
	Net primary productivity	1.51	2.96	2.07	4.06	1.52	2.98	1.70±0.2	3.33±0.4

* based on growing seasons of: 55 days-1971, 45 days-1972, 55 days-1973.
** based on actual area (51%) of the meadow vegetated and on total (100%) area vegetated.
*** based on sampling depth of 20 cm from the moss surface.

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Table 19. Average vascular plant net primary production (g/m^2±stnadard error) and seasonal primary productivity (g/m^2/day±standard error) at the wet (site 18) sedge-moss meadow 1971 - 1973.

Plant Group	Component	Growing Season 1971	1972	1973	Average
Monocots	Green	38.9	36.9	37.2	37.7±0.6
	Non-green	5.7	6.7	6.6	6.3±0.3
	Rhizomes	7.1	9.3	6.2	7.5±0.9
	Roots**	121.8	119.0	119.6	120.5±6.5
Forbs	Green	1.8	1.3	1.1	1.4±0.2
	Roots	0.8	1.4	0.8	1.0±0.2
Woody Plants	Green	—	—	—	—
	Non-green	—	—	—	—
	Roots	—	—	—	—
TOTAL	Net aboveground production	46.4	44.9	44.9	45.4±0.5
	Net belowground production	129.7	129.7	126.6	128.7±1.0
	Total net production	176.1	174.6	171.5	174.1±8.8
	Ratio above:below	1:2.8	1:2.9	1:2.8	1:2.8
	Aboveground primary productivity	0.84	0.99	0.82	0.88±0.1
	Belowground primary productivity	2.36	2.88	2.30	2.51±0.2
	Net primary productivity	3.20	3.87	3.12	3.39±0.2

* based on growing seasons of: 55 days-1971, 45-1972, 55-1973.

** based on sampling depth of 20 cm from the moss surface.

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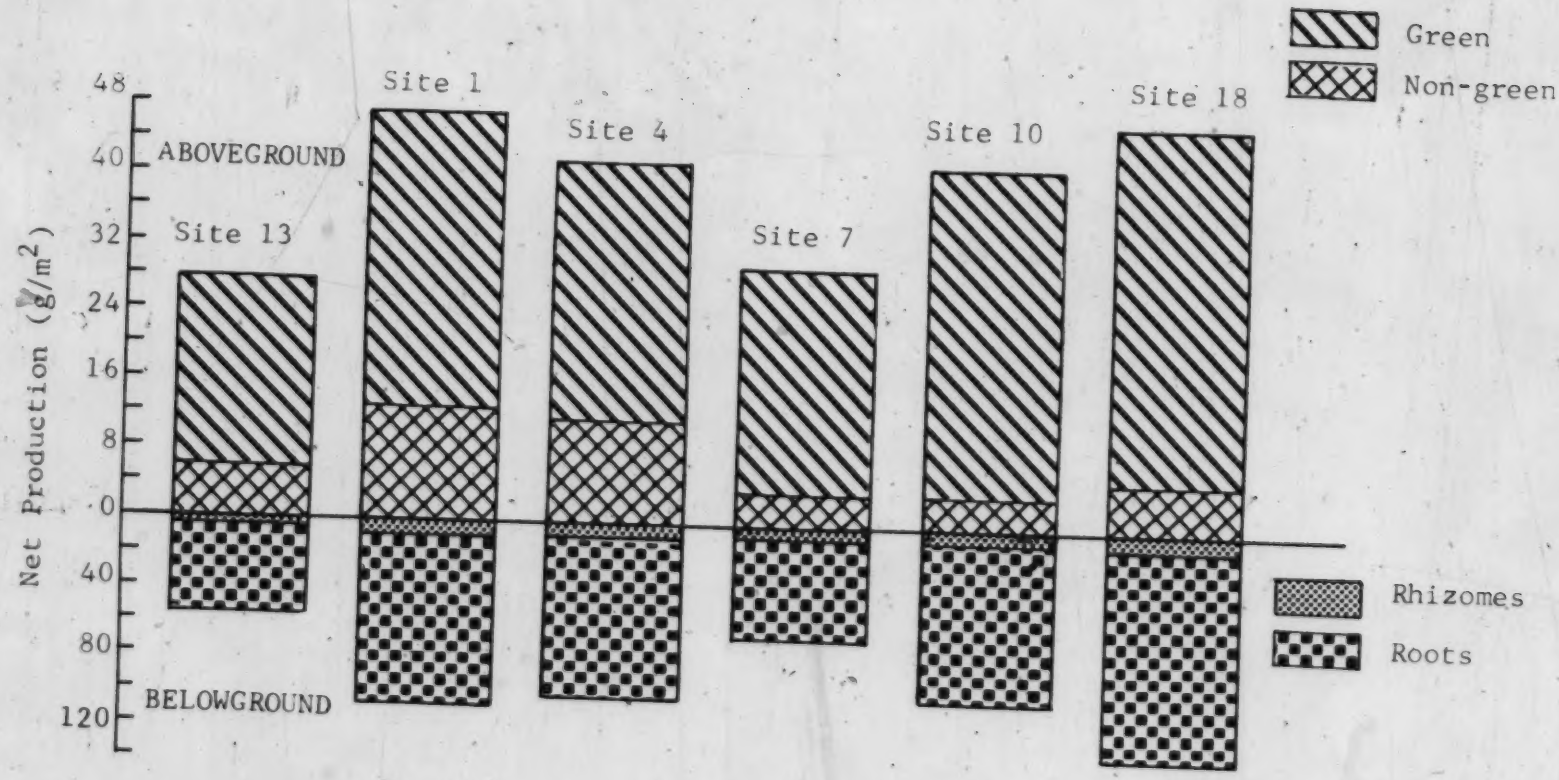

Figure 29. Net aboveground and belowground primary production (g/m^2) in a frost-boil (site 13), hummocky (sites 1,4,7,10), and wet (site 18) meadow 1971.

tissue production (41 g/m^2) and the hummocky intensive study meadow the highest non-green tissue production (13 g/m^2).

On the basis of a totally vegetated meadow surface area, aboveground production in the frost-boil meadow would have been on the order of 54 g/m^2. It is more likely that the actual production would more closely approximate an average production (42 g/m^2) of a hummocky meadow.

Greenhouse production data indicated a 26% increase in aboveground production over that found in the controls.

Mean annual aboveground production in the lowland meadows had an annual variation of less than 5%, with variation in the monocot component being ca. 10% and ca. 20% in the forbs and woody plants. At the hummcoky intensive study (site 1) meadow aboveground production was only 10% higher in an earlier and milder season (1971) than in a later and cooler (1970,1972) season. The reverse trend was found in the frost-boil meadow and production remained fairly consistant from year to year in the wet meadow.

Aboveground productivity (g/m^2/day) over the course of the potential growing season provided a more accurate indication of seasonal plant growth. The potential growing season was taken from the time of leaf growth initiation (late June - early July) to the time of 50% leaf senescence (mid-August). Correction factors were included for pre-peak dieback and post-peak growth.

The highest average productivity was found in the wet meadow (0.88 ± 0.1 g/m^2/day) and the lowest was in the frost-

boil meadow (0.54±0.1 g/m^2/day). Mean annual productivity of the hummocky intensive study meadow was 0.87±0.1 g/m^2/day and ranged from a low of 0.85 g/m^2/day in 1970 and 1971 to a high of 0.99 g/m^2/day in 1972. Corresponding data for the frost-boil and wet meadow were minima of 0.46 and 0.82 g/m^2/day, respectively, and maxima of 0.67 and 0.99 g/m^2/day, respectively. Interestingly enough, aboveground production was highest in a later and cooler season (1972) when the potential growth period was 10 days shorter than that in an earlier and milder season. In 1972, productivity was ca. 20% higher in the hummocky and wet meadow and ca. 40% higher in the frost-boil meadow.

Belowground

1. Composition and distribution.

Determination of belowground standing crops was more difficult than estimating aboveground biomass. An overall uniformity in meadow vegetation cover; contribution of the major portion of the root biomass by one plant group - monocots; and concentration of the rooting zone in the upper 25 cm of the soil profile, helped to keep sample variability down. Variation nevertheless was on the order of 20 - 30% as compared to the 10 - 15% found for aboveground samples.

In the hummocky intensive study (site 1) meadow 85% of the belowground biomass was in the upper 20 cm of the soil (Table 20).

Table 20. Vertical root biomass (g/m^2) distribution (%) and standard error (±) under hollow, hummock, and combined habitats in the hummocky intensive study (site 1) meadow August 1973 (n=18).

Sample Depth (cm)	Meadow Habitat		
	Hollow	Hummock	Combined
Moss (0 - 5)	5.9±1.7	4.2±1.3	5.1±3.4
Soil (5 - 10)	30.6±5.5	32.5±2.1	31.5±3.8
(10 - 15)	27.3±3.0	29.0±5.1	28.2±4.2
(15 - 20)	22.4±3.8	20.4±3.8	21.4±4.2
(20 - 25)	13.8±5.9	13.9±3.8	13.8±5.1

Vertical root distribution did not differ significantly under the hummock and hollow habitats. Forb and woody plant roots, as well as monocot rhizomes, were concentrated in the upper 5 cm of the moss/ soil layer. The vertical distribution of roots in the hummocky meadow was considered to be representative of distributions in the other two meadow community types.

Hummock root biomass at both the hummocky (site 1) and frost-boil (site 13) meadow was 50 and 35% higher, respectively, than hollow root standing crops. In the frost-boil meadow root biomass beneath the heavily vegetated areas of the meadow was 400% greater than that found in the frost-boils. All meadow root biomass estimates were made on a combined microhabitat basis, calculated on the proportional surface area cover by each microhabitat.

At the hummocky and frost-boil meadow approximately 96% of the belowground biomass was contributed by monocots, 3%

by woody plants, and 1% by forbs. At the wet meadow, monocots developed 99% of the belowground biomass and forbs the remaining 1%. Rhizomes, in each of the meadows, constituted less than 5% of the total belowground biomass.

Visual sorting of the monocot roots into live and dead components was histochemically proven to be accurate for the live component but inaccurate in the dead component. Of the roots identified as being dead, 15±2.3% were tested as being viable (live). The appropriate correction factor was applied to all the divided root samples. The resulting seasonal live:dead monocot root ratio was 52% live:48% dead. The live:dead root ratios remained fairly constant both intra- and inter-seasonally (Fig. 30).

2. Biomass.

Average peak season belowground standing crops were highest in the hummocky intensive study (site 1) meadow (2034±74.3) and lowest in the frost-boil (site 13) meadow (651±24.3 g/m^2) (Fig. 31). The wet (site 18) meadow belowground biomass averaged 1367±72.7 g/m^2. Living plant material made up 55% of the total biomass. Of the rhizome material, live rhizomes were 225 - 515% higher in their contribution than were dead rhizomes. Rhizome increment was 13%.

Seasonal belowground biomass increment, as shown by the 1972 data, corresponded to seasonal soil thaw development (Fig. 32). Maximum biomass levels were found by mid-August when soil thaw was deepest.

On a seasonal (1971) comparison the hummocky meadows

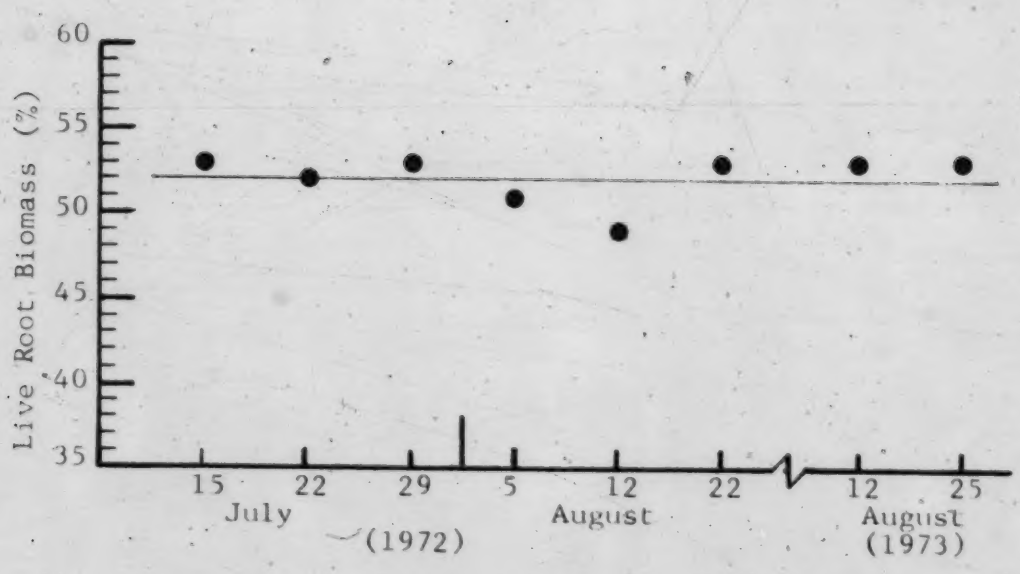

Figure 30. Seasonal monocot live root biomass (%) component of the total monocot root biomass (hummocky intensive study (site 1) meadow) 1972 - 1973.

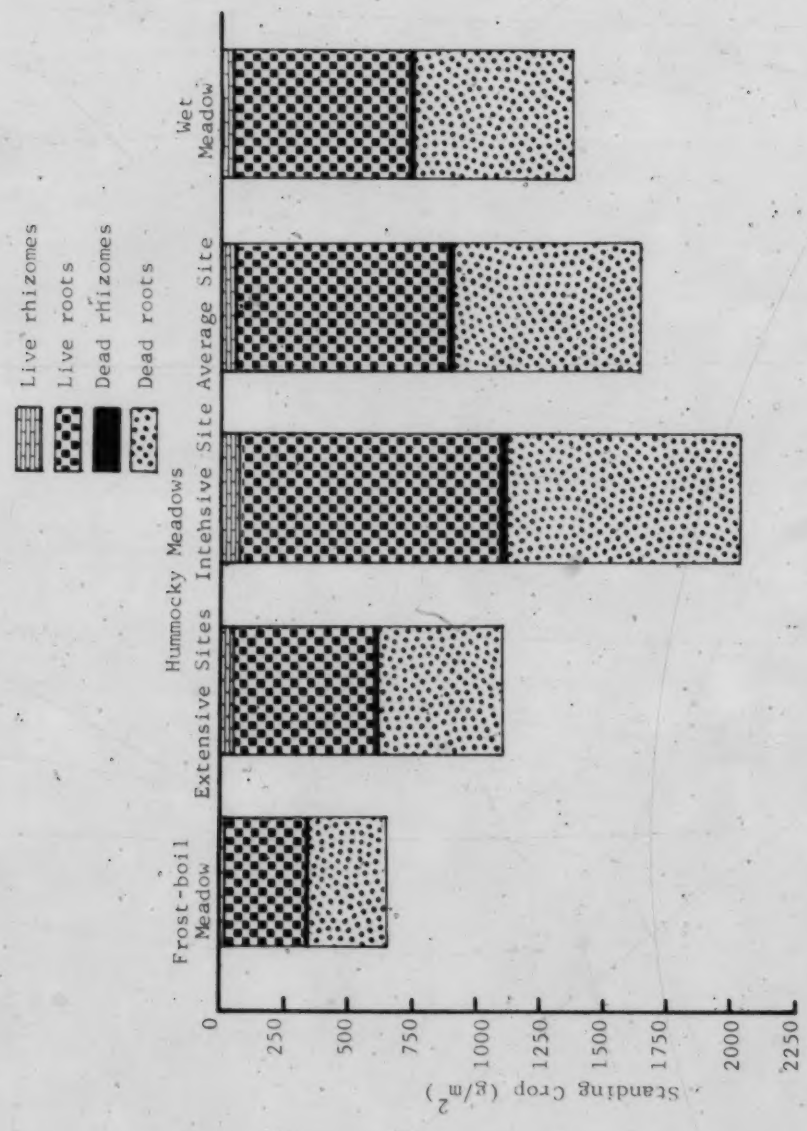

Figure 31. Peak season belowground standing crops (g/m^2) in a frost-boil (site 13), hummocky (sites 1,4,7,10), and wet (site 18) sedge-moss meadow (based on 1 - 4 yrs data).

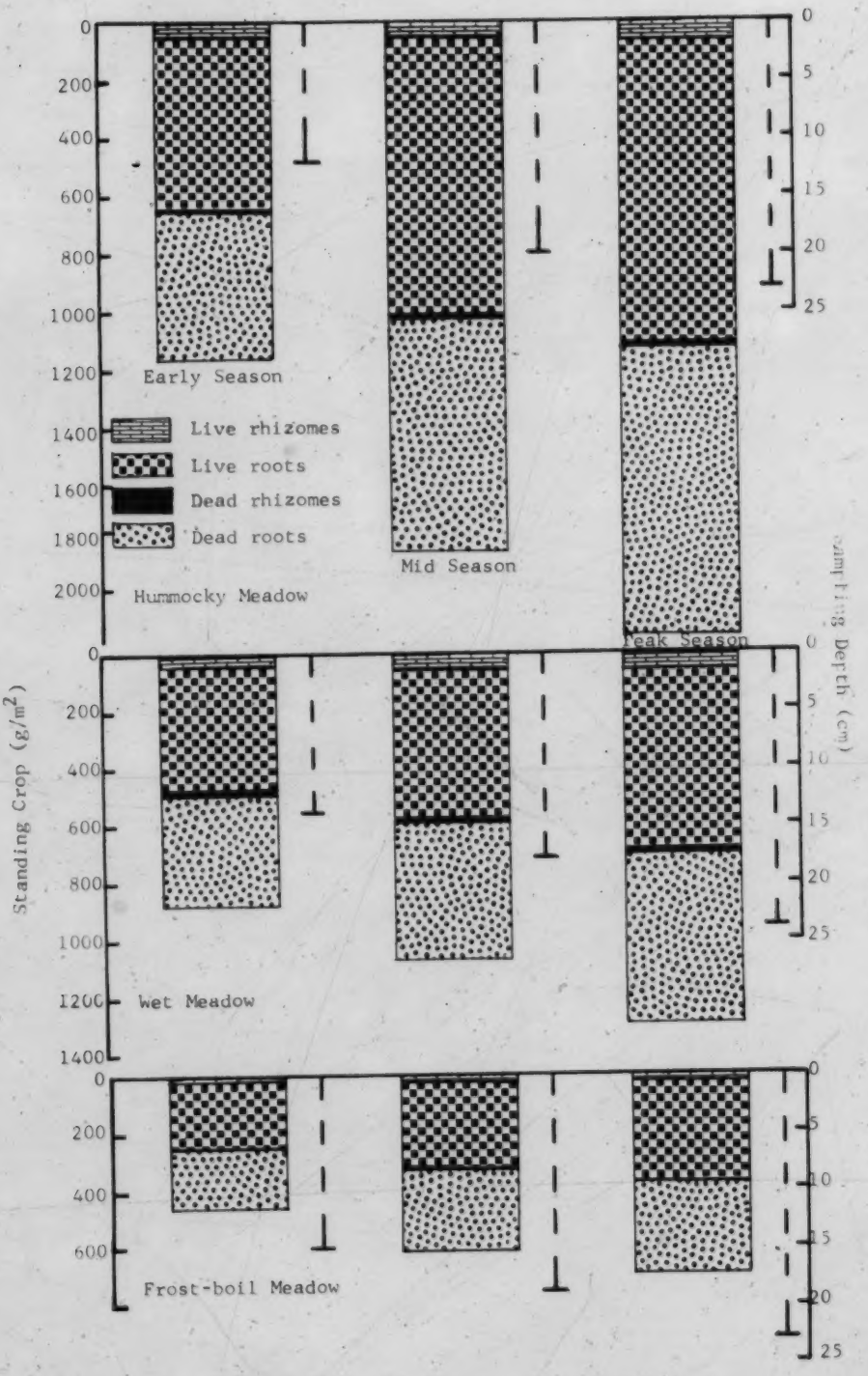

Figure 32. Belowground standing crops (g/m^2) and sampling (=thaw) depths (cm) in early (early July), mid (late July), and peak (mid August) season, at the hummocky (site 1), frost-boil (site 13), and wet (site 18) sedge-moss meadow 1972.

(site 1,4,7,10) had belowground biomass levels 40 - 220% greater than those in the frost-boil (site 13) meadow (Fig. 28). Only the intensive study (site 1) and rock-base (site 4) meadow, both underlain by Fibric Organo Cryosols, had greater (55 and 10%, respectively) belowground standing crops than were found in the wet (site 18) meadow. The plateau-base (site 10) and coastal (site 7) hummcoky meadow, both underlain by Gleysolic Static Cryosols had the lowest belowground biomasses of any hummocky meadow. These were still 40 - 55%, respectively, greater than those of the frost-boil meadow.

Seasonally, belowground biomass peaked by early to mid-August when aboveground biomass was at its peak and when soil thaw was at its maximum. Inter-seasonal belowground standing crop variation was approximately 10% (Table 14).

3. Net production.

Average seasonal (1970 - 1973) belowground net production and productivity data are presented in Table 15. Corresponding seasonal data are presented in Tables 16, 17, 18, and 19.

The average seasonal meadow belowground production closely paralleled the meadow moisture gradient. The flooded wet (site 18) meadow had an average production of 129 ± 1.0 g/m^2 and the slightly moist frost-boil (site 13) meadow only 59 ± 2.3 g/m^2. The average lowland hummocky (site 1,4,7,10) meadow production was 97 ± 5.6 g/m^2 and was 103 ± 2.4 g/m^2 at the intensive study (site 1) meadow. Meadow below-

ground production was highest in 1972 but even then was only 5% higher than it had been in any of the other years.

Monocot root and rhizome material contributed 94% of the belowground production, with rhizomes constituting 5% of this total. Woody plant roots contributed 5% of the production and forbs the remaining 1%.

The seasonal (1971) 'in situ' root weight increment of Carex stans tiller transplants was 24.2±3.7% of the original attatched root biomass. This increment would be equivalent to the root growth occurring in the upper 10 cm of the soil profile. Of this root increase, 46% occurred in the formation of lateral roots off existing roots; 33% in the form of new roots; and 21% as the elongation of existing roots. All the transplanted tillers developed a full leaf compliment which suggested that any adverse effects of transplantation were minimal.

Belowground seasonal mean productivity was also highest in the wet meadow (2.51±0.2 $g/m^2/day$) and lowest in the frost-boil meadow (1.16±0.1 $g/m^2/day$). Average productivity of the lowland hummocky (site 1,4,7,10) meadows was 1.84±0.1 $g/m^2/day$ and averaged 2.02±0.1 $g/m^2/day$ in the hummocky intensive study (site 1) meadow. On a seasonal (1971) basis, the intensive study meadow's productivity was 20% higher than that of any of the other hummocky meadows. The highest meadow belowground productivity was recorded in 1972 ,, being 30% greater than in any of the other seasons.

Meadow Totals

1. Biomass

On a comparative total standing crop basis hummocky (sites1,4,7,10) meadows maintained the highest average biomass (1892 g/m^2) and the frost-boil meadow the lowest (821 g/m^2) (Table 21). The wet (site 18) meadow's average biomass was 1570 g/m^2. The highest recorded meadow biomass of 2316 g/m^2 was found at the hummocky intensive study (site 1) meadow.

On a seasonal (1971) comparison of lowland meadows, the hummocky (sites 1,4,7,10) meadows had 35 - 190% more biomass than the frost-boil (site 13) meadow (Fig. 28). The standing crops of the intensive study (site 1) and rock base (site 4) meadows was 50% and 10%, respectively, greater than the wet (site 18) meadow's biomass. The wet meadow had 90% more biomass than the frost-boil meadow and 45% and 20% more thanthe plateau-base (site 10) and coastal (site 7) hummocky meadows, respectively.

Total live aboveground:live belowground standing crop ratios were 1:6.0 in the frost-boil meadow and 1:9.1 in the wet meadow. The average ratio for the hummocky (sites 1,4,7, 10) meadows was 1:10.8 and was 1:12.8 in the intensive study (site 1) meadow.

Total dead aboveground:belowground standing crop ratios averaged 1:2.7 at the frost-boil meadow and 1:5.2 in the wet meadow. The hummocky meadows' average was 1:4.2 , with 1:4.8 at the intensive study meadow.

Table 21. Average peak season vascular plant standing crops (g/m^2 ±standard error) in a frost-boil (site 13), hummocky intensive study (site 1), average hummocky (sites 1,4,7,10), and wet (site 18) sedge-moss meadow 1970 - 1973. A calculation is also made for a representative* lowland sedge-moss meadow.

Component	Frost-boil	Sedge-moss Meadow			Representative Lowland Meadow
		Intensive Study Meadow	Average Hummocky	Wet	
ABOVEGROUND					
Green	27.1±0.9	36.0±0.9	38.3±2.0	40.0±1.1	33.4
Non-green	30.1±1.8	49.6±2.3	43.3±3.8	37.2±2.3	37.2
Total live	57.2±1.0	85.6±2.4	81.6±2.6	79.7±2.3	70.6
Attatched dead	101.7±3.8	184.2±5.9	164.5±13.9	117.7±5.4	134.0
Litter**	10.7±1.9	12.5±1.8	12.1±1.1	5.3±0.3	11.1
Total dead	112.4±5.7	196.7±7.7	176.6±15.0	123.0±5.7	145.1
Grand total	169.6±4.9	282.3±3.5	258.2±15.3	202.7±22.3	215.7
Live:dead	1:1.8	1:2.3	1:2.2	1:1.5	1:2.1
BELOWGROUND					
Live rhizomes	17.3±0.3	58.1±1.3	54.8±2.5	50.0±2.2	37.7
Live roots	328.1±12.3	1033.4±38.3	827.0±104.1	672.3±39.2	594.8
Total live	345.4±12.2	1091.5±39.4	881.8±106.2	727.3±30.9	632.5
Dead rhizomes	3.1±0.4	10.6±0.2	9.0±0.9	13.7±1.4	6.6
Dead roots	302.4±10.6	931.7±35.4	742.5±95.1	625.8±36.9	538.6
Total dead	305.5±12.1	942.3±35.4	751.5±95.9	639.5±35.6	545.2
Grand total	650.9±24.3	2033.8±74.3	1633.2±202.1	1366.8±72.7	1177.7
Live:dead	1:0.9	1:0.9	1:0.9	1:0.9	1:0.9
Grand Total	820.5	2316.1	1891.5	1569.5	1393.4
Live above:below	1:6.0	1:12.8	1:10.8	1:9.1	1:9.0
Dead above:below	1:2.7	1:4.8	1:4.2	1:5.2	1:3.8
Total above:below	1:3.8	1:7.2	1:6.3	1:6.7	1:5.5

* based on lowland area occupied by each meadow type (hummocky-50%, frost-boil-45%, wet-5%)

** based on peak litter standing crops which developed at the start of the growing season.

Peak season total aboveground:belowground biomass ratios averaged 1:3.8 in the frost-boil meadow and 1:6.7 in the wet meadow (Table 21). The hummocky meadows' average ratio was 1:6.3 and 1:7.2 at the intensive study meadow.

2. Net production and productivity.

Seasonal data of average net production and productivity are presented in Table 15. Each meadow's annual estimates are presented in Tables 16, 17, 18, and 19.

The highest total production of the lowland meadows was found in the wet meadow (174±8.8 g/m^2/day) and was lowest in the frost-boil meadow (87±3.4 g/m^2/day). The lowland hummocky meadows averaged 138±7.6 g/m^2/day, with the average for the intensive study meadow being 147±3.4 g/m^2/day. The highest annual production in the hummocky and wet meadows occurred in 1971, with increments of 6% and 2%, respectively, over those found in other years. A similar comparison for the frost-boil meadow revealed the highest production being in 1972 and being 7% lower in 1971.

Belowground production was on the average 115 - 185% greater than the aboveground production. This served as an indication that the majority of the assimilated carbon was being converted into belowground production.

On a seasonal (1971) comparison of the lowland meadows the wet meadow was the most productive (176 g/m^2) and the frost-boil meadow the least productive (83 g/m^2) (Fig. 29). A comparison of the hummocky (sites 1,4,7,10) meadows showed the intensive study meadow to have the highest

production (154 g/m^2) and the coastal (site 7) meadow to be the least productive (94 g/m^2).

Total meadow productivity averaged 3.39±0.2 g/m^2/day in the wet (site 18) meadow and 1.70±0.2 g/m^2/day in the frost-boil meadow (site 13). Hummocky (site 1,4,7,10) meadow productivity averaged 2.63±0.2 g/m^2/day and was 2.89±0.2 g/m^2/day in the intensive study (site 1) meadow. The highest annual productivity was recorded in the short (45 day) 1972 growing season. Productivity was highest at the wet meadow (3.87 g/m^2/day) and lowest in the frost-boil meadow (2.07 g/m^2/day). The equivalent productivity at the hummocky intensive study meadow was 3.37 g/m^2/day.

Discussion

Aboveground

1. Biomass.

Pre-peak dieback and post-peak growth were of minor importance in the frost-boil and hummocky intensive study meadow's production (2% and 6%, respectively) but played a greater role (12%) in the wet meadow's production. Pre-peak dieback occurred in the old overwintering leaves and post-peak growth occurred in the 'young' leaves initiated during the course of the growing season. During the growing season lemming (Dicrostonyx groelandicus) utilization (grazing) of the lowland meadows was minimal (Speller 1972) and intensive muskoxen grazing was restricted to specific areas of the lowland (Hubert 1976). No signs of grazing were found in the meadows sampled for production.

Whitfield (1976) estimated lowland meadow standing crop removal by herbivore grazing to be only 1 - 2%. Even during a period (1973) with high lemming populations intensive grazing of meadow plants was not evident.

The relatively short, 50 day average, meadow growing season minimized variation in time of peak biomass development within the meadow plant groups. Although woody plants and forbs put on a full leaf compliment two weeks earlier than monocots, biomass peaks in all three groups were relatively synchronous. Similar synchrony in plant group biomass peaks was found in the rock outcrop (dwarf shrub-heath-moss) communities (Bliss and Kerik 1973). In the Barrow meadow peak monocot biomass levels were formed earlier than similar peaks in forbs (Dennis and Tieszen 1972).

Overwintering meadow monocot and forb green tissue averaged 6 g/m^2. This green component was of 'young' leaves which had overwintered in a green state. The overwintering tissue experienced less than 10% post-snowmelt deterioration and provided the meadow plants with an immediate photosynthetic capacity. Mayo et al. (1976) found Carex stans tillers capable of photosynthesizing at low temperatures similar to those found in the early spring. Barrow meadow monocots also overwintered with a significant (10 g/m^2) green tissue component but the tissue deteriorated (photo-oxidation?) readily after snowmelt (Dennis and Tieszen 1972).

Seasonal increment in monocot green biomass closely

paralleled seasonal leaf growth (Fig. 33). A similar relationship was found with chlorophyll content and to a lesser degree with photosynthetic leaf area (Fig. 34). Meadow canopy components were closely synchronized in their development as a result of the shortness of the growing season. They exhibited a fairly linear pre-peak increment and an equally linear post-peak decline. In the Barrow meadow, chlorophyll content and aboveground biomass showed similar seasonal correlations (Dennis and Tieszen 1972, Tieszen 1972a).

The major (30 - 80%) portion of the early season aboveground biomass was of non-green tissue. Monocot stem bases; woody plant stems; and forb taproots served as sources of early season energy reserves for the growing leaf primordia. The greater average concnetration of aboveground live biomass in the hummocky (site 1) meadow (86 g/m^2) as compared to the frost-boil (site 13) meadow (57 g/m^2) was in large part due to the higher (100%) stem densities found in the former meadow. Although the stem density of the wet (site 18) meadow was only 60% that of the hummocky meadow, its high standing crop (80 g/m^2) was due to an almost mono-specific growth (Carex stans) and optimal growth conditions for this semi-aquatic species. Inter-hummocky meadow aboveground live biomass variation was proportional to environmental temperature regimes and soil conditions. The warmer intensive study (site 1) hummocky meadow, underlain by an organic soil, had a 15% higher biomass content than was found in the colder

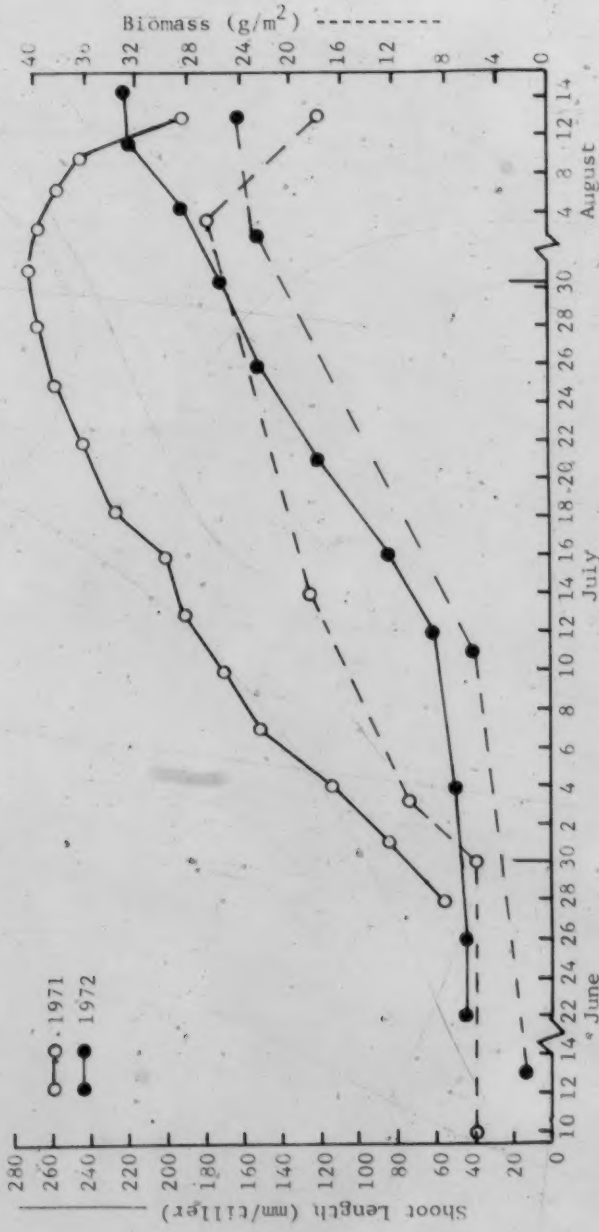

Figure 33. Seasonal monocot green shoot length (mm) and biomass (g/m^2) increment at the hummocky intensive study (site 1) meadow 1971, 1972.

Figure 34. Seasonal development of community chlorophyll (mg/m^2), green leaf area index, and green leaf biomass (g/m^2) at the hummocky intensive study (site 1) meadow 1971.

coastal (site 7) hummocky meadow underlain by a gleysolic soil.

Lowland meadow aboveground live standing crops were very similar to those reported for related low arctic meadow communities in other regions (Table 22). It is questionable as to whether these cited studies included the non-green component in their live biomass data. On a strictly green biomass (45 - 50% of the total live material) comparison, high arctic meadows had 60 - 550% less biomass than did the low arctic meadows. The northern extension of these low arctic communities resulted in a decrease in their standing crops brought about by a reduction in community plant density. Stem densities at Barrow (Dennis and Tieszen 1972) were 120 - 335% higher than those in lowland meadows and correspondingly its green biomass levels were 120 - 220% higher.

The relatively high (25%) early season litter component in the aboveground total biomass supported the phenological evidence that the meadow monocot leaves remained attatched for al least five years and then became incorporated into the litter. Little (0.1%) of the litter was removed from the meadows by spring meltwaters. Average peak season total aboveground standing crops were 282 g/m^2 at the hummocky intensive study (site 1) meadow; 203 g/m^2 at the wet (site 18) meadow; and 170 g/m^2 at the frost-boil (site 13) meadow. Of the aboveground biomass, 60 - 70% was within the moss layer. Similarily, 65 - 75% of the aboveground dead plant

Table 22. Maximum aboveground standing crops (live and total, g/m^2) in tundra communities of other regions, comparable to those of the lowland sedge-moss meadows.

Location	Community	Standing Crop Live*	Standing Crop Total**	Reference Source
Truelove Lowland, Devon Island, N.W.T.	Frost-boil meadow	57	170	
	Hummocky meadow	82	258	
	Wet meadow	80	203	
Barrow, Alaska	Meadow tundra	89	231	Tieszen (1970)
Prudhoe Bay, Alaska	Meadow tundra	95	287	Tieszen (1970)
Dempster Highway, Yukon	Cottongrass tussock dwarf-shrub heath	66	168	Wein and Bliss (1974)
Mackenzie Delta, N.W.T.	Wet sedge meadow	73	195	Haag (1974)
Western Taimyr, U.S.S.R.	Spotted tundra	90	107	Khodachek (1969)
	Hummocky tundra	99	149	
	Polygonal (wet?) tundra	189	234	
Bol'shoj Ljakhovskig Island, U.S.S.R.	Tussock spotted tundra	71	140	Aleksandrova (1970b)
	Polygonal moss-grass tundra	49	110	

* Truelove Lowland meadow data based on green and non-green tissues.
** Truelove Lowland meadow data include shoot and stem base components.

material was retained in the moss layer. Retention of a large proportion of the aboveground standing crop within the moss layer insured significant nutrient retention within the meadow ecosystem. This helped to compensate for the low nutrient levels occurring within the lowland meadows (Babb and Whitfield 1976).

Rock outcrop dwarf shrub-heath-moss communities (Bliss and Kerik 1973) maintained aboveground total standing crops (vegetated areas) which were 35 - 270% higher than those in the meadows. Plant growth in these communities was restricted to 32% of the total habitat and on a total area basis the standing crop was up to 60% less than that of the meadows. Raised beach cushion plant communities had 75 - 105% more biomass than the meadows (Svoboda 1973) with dead Dryas integrifolia leaves responsible for the increased biomass. In the raised beach communities the growth strategy was one of retention of the majority of the plant tissue aboveground. Compared to low arctic meadow communities of other regions, lowland meadows shared a similar total aboveground biomass (Table 22). On a strictly above moss surface basis, assuming that the cited data may have been expressed on only this component, the lowland meadows had 10 - 265% less biomass than their low arctic counterparts. Lower plant densities; less vigorous plant growth; and lower plant canopy heights would help explain the lower standing crops found in high arctic meadows. The high biomass contribution (85 - 95%) by monocot species was also a significant factor in the lower

biomass. Haag (1974) found that standing crops of monocot dominated communities in the low arctic were 30% lower than in communities with a larger woody plant input.

2. Net production.

Meadow aboveground production peaks occurred 40 - 50 days after snowmelt (early to mid-August). Seasonal production developed in proportion to the warmer temperatures and high incoming radiation levels measured (Courtin and Labine 1976) over the growing season. Post-peak production climatic conditions were marked by low temperature conditions and lower incoming radiation levels. Corresponding 40 - 50 day post-snowmelt production peaks were also reported (Pieper 1963, Tieszen 1970) for the Barrow meadows. Arctic meadow plants, irrespective of their low or high arctic location, appeared to maintain a similar growth period. It was not determined if this was due to genetic or environmental factors.

Aboveground production in the lowland meadows followed a distinctive moisture gradient (frost-boil to wet meadow). The wet meadows maintained flooded conditions throughout the growing season and provided the sedges with their most optimal growth habitat. Over the three seasons of production sampling, their average production was 45 g/m^2. The frost-boil meadows had only a moist habitat and their less favorable sedge growth conditions limited their average production to 28 g/m^2. Over 75% of the aboveground production was of green plant material. Monocots made the main (70%) contri-

bution to the aboveground production.

Low meadow species diversity; comparable plant growth dynamics from year to year; and a low (1 - 2%) grazing stress contributed in developing minimal (< 5%) variation in annual aboveground production. Meadow plant growth (=production) did not appear significantly affected by annual changes in the climatic conditions during the growing season. Svoboda (1973) also found a similar low annual variation in aboveground production in the raised beach cushion plant communities. High arctic plant growth appeared to be adapted to minimum growth requirements. In the earlier and warmer 1971 season, production at the hummocky (site 1) and wet (site 18) meadows was only 10% greater than that in a later and cooler season but in a similar comparison was depressed by 10% at the frost-boil (site 13) meadow. The deeper soil thaw and the associated increase in soil drainage may have been responsible for the slight production decrease in the frost-boil meadow. The pronounced seasonal production fluctuations reported for low arctic meadows (Pieper 1963, Dennis and Johnson 1970) were associated with fluctuating grazing intensities. This was not the case in the lowland meadows.

On a comparative basis, lowland meadow aboveground production was comparable to that of low arctic meadows (Table 23). Only when compared to the most southern low arctic communities was it 115 - 245% lower. The higher production of these sites is derived from a denser plant cover and a more optimal and longer growing season.

Table 23. Net aboveground vascular plant production (g/m^2) in tundra communities of other regions, comparable to those of the lowland sedge-moss meadows.

Location	Community		Production* (g/m^2)	Reference Source
Truelove Lowland, Devon Island, N.W.T.	Frost-boil meadow		28	
	Hummocky meadow		42	
	Wet meadow		45	
Barrow, Alaska	Meadow tundra	(1961)	33	Pieper (1963)
		(1962)	45	
	Meadow tundra	(1964)	60-97	Dennis and Johnson
		(1965)	3-48	
	Sedge grass meadow		102	Tieszen (1972a)
	Carex meadow		51-91	Shanks (as cited by Bliss 1962a)
Umiat, Alaska	Carex-Eriophorum meadow		60	Bliss (1956)
Eagle Creek, Alaska	Cotton grass tussock dwarf-shrub heath	(1968)	65	Wein and Bliss (1974)
		(1969)	77	
		(1970)	75	
Dempster Highway, Yukon	Cotton grass tussock dwarf-shrub heath	(1968)	35	Wein and Bliss (1974)
		(1969)	38	
		(1970)	43	
Meade River, Alaska	Graminoid tundra		82	Johnson and Kelley (1970)
Mackenzie Delta, N.W.T.	Wet sedge meadow		73	Haag (1974)
Western Taimyr, U.S.S.R.	Spotty tundra		15	Vassiljevskaya and Grishna (1972
	Marshy tundra		30	

*Truelove lowland meadow data based on green and non-green components.

The meadow field greenhouses, with average air temperatures 7° C higher than those outside the greenhouse, increased their aboveground production by 26%. This compared favorably with the increases measured for monocot chlorophyll, photosynthetic leaf area, and flowering levels. The increased production was probably due to increased photosynthetic rates developed by the increase in air and corresponding leaf temperatures. Such temperature increases were over 50% higher than the variation in growing season temperatures found from year to year.

It was not determined to what extent the increased aboveground production was based on the expense of belowground carbohydrate reserves. If this actually did occur to one degree or another, it would have produced a negative net effect. Belowground reserves are vital to the meadow plants in insuring a rapid growth pattern early in the season. Svoboda (1974) and Tieszen (1970) found similar growth increments in their raised beach and low arctic meadow, respectively, greenhouses.

Lowland meadow aboveground productivity ranged from 0.54 g/m^2/day in the frost-boil (site 13) meadow to 0.88 g/m^2/day in the wet (site 18) meadow. This would place the lowland meadows' productive capacities at the lower range of Bliss' (1962a) predicted 1 - 3 g/m^2/day aboveground productive capacity for tundra communities. This was to be expected since these high arctic meadows are extensions of similar low arctic communities.

Belowground

1. Biomass.

The majority (96%) of the meadow belowground biomass consisted of monocot tissue. Of the total biomass, 85% was concentrated in the upper 20 cm layer of the soil profile. These root concentrations corresponded to higher soil temperatures, better soil aeration, and greater nutrient availability (Walker and Peters 1976). Soil thaw was also earlier and longer in duration in the upper soil profile. The strategy of concentrating root biomass in the upper part of the soil appears to be characteristic of both high arctic and low arctic (Tieszen 1970, Khodachek 1969, Evodkimova et al. 1968, Aleksandrova 1970a, Pavlova 1969).

Although vertical root concentrations below hummock and hollow habitats were similar, poorer growth conditions in the hollow soils resulted in standing crops 35 - 50% lower than those beneath hummocks. The estimated root production within hummocks (5.3%) was only slightly higher than that in hollows (4.8%). Lower root standing crops within the frost-boil soils, compared to those beneath vegetated areas, corresponded to a lower plant cover and poor root growth environments. The frost-boil soils are highly alkaline and possess low levels of available nutrients (Walker and Peters 1976).

Belowground root biomass was almost equally divided into live (52%) and dead (48%) components. The 15% viable root component in visually classified dead roots was

considered to comprise roots which were in the latter stages of dying. Although arctic meadow and temperate grassland communities have different rooting strategies, a similar live:dead root ratio has been established (Clark 1974) for these latter communities by means of ^{14}C.

The viable (live) root component of the dead root biomass indicated that monocot root lifespans were on the order of *ca.* 5 - 8 years and that roots outlived tillers by 1 - 3 years. The advantage of delayed root mortality would insure that the energy reserves of the dead and dying tillers could be transferred to developing tillers. Such a belowground utilization of photosynthetic and nutrient resources would compensate for the poor nutrient status of meadow soils. The availability of an established rooting system would also insure a greater survival rate in developing tillers.

In low arctic *Carex aquatilis*, root life spans were calculated to be 5 - 8 years (Shaver and Billings 1975). *Eriophorum angustifolium* was found to replace its rooting system annually and this may have contributed to the greater longevity (*ca.* 7 years) of its tillers.

The large dead root component of the meadow belowground biomass was attributed to the lower soil decomposition rates which developed under conditions of low soil temperature and poor soil aeration. This resulted in an accumulation, rather than complete breakdown, of dead root material. Widden (1976) found maximum meadow microbial populations to

be concentrated in the upper 5 cm layer of the soil profile and for microbial levels to be considerably lower at lower depths.

The high live component in the belowground biomass indicated longer root lifespans and possible involvement in tillering. The extensive (65 - 70%) occurence of tiller clumping suggested tiller interdependence. Dying tillers appeared to give rise to new tillers by means of short ($<$ 10 mm) rhizomes and their roots would have served the immature tillers until they had established their own root systems. Shaver and Billings (1975) have reported similar belowground strategies for low arctic Carex aquatilis.

Seasonal belowground standing crops increased in proportion to the depth of soil thaw. Maximum standing crops developed by early to mid-August. Roots in the upper 10 - 15 cm layer of the soil had a longer (ca. 50 - 75%) growth period than did roots at depths of 20 - 25 cm. The majority of root growth occurred in the upper soil profile.

Rhizome standing crops changed less than 15% over the course of the season. Peak rhizome biomass developed in conjunction with aboveground biomass peaks. This would indicate that belowground translocation of photosynthates was most pronounced toward the latter part of the growing season.

The hummocky meadows had the highest average belowground biomass (1633 g/m^2). Their root biomass varied considerably

from meadow to meadow and was found to be dependent on the soil type. The moist, warm, and organic Fibric Organo Cryosols of the hummocky intensive study (site 1) meadow had an average root biomass of 2034 g/m^2. The wet, cold, and more mineral Gleysolic Static Cryosols of the coastal (site 7) and plateau-base (site 10) hummocky meadow had less than one-half the root biomass. Their belowground biomass was also only 35 - 55% greater than the 651 g/m^2 average root biomass of the frost-boil (site 13) meadow.

Similarily, excessive soil moisture levels in organic Fibric Organo Cryosols create a poor rooting environment. Stagnant soil water conditions at the wet (site 18) meadow helped reduce root biomass to an average 1367 g/m^2. Low soil nutrient availability in this meadow (Walker and Peters 1976) would also have contributed to its lower root biomass.

In the lowland plant communities, belowground standing crops increased along an increasing soil moisture gradient. High root biomasses were found in the hummocky meadows and low standing crops in the dry and nutrient-poor soils of the raised beach cushion plant communities. In these latter communities, maximum biomass was concentrated aboveground. The mesic soil conditions of the rock outcrop dwarf shrub-heath communities favored higher root standing crops and in the vegetated areas these ranged from 895 - 1135 g/m^2 (Bliss and Kerik 1973).

Belowground standing crops of comparable low arctic

communities in other regions were up to 435% greater than those of the lowland sedge-moss meadows (Table 24). These higher low arctic root standing crops undoubtedly reflected greater plant densities, and longer and more favorable growth conditions in deeper thawing soils.

2. Net production.

Net belowground production accounted for 70% of the total meadow production. Such high concentrations of assimilates belowground insured meadow plants the necessary energy reserves for initiating early season growth. At Barrow, Tieszen (1972b) found that monocots translocated approximately 75% of their fixed carbon belowground. This would indicate that belowground translocation of a major portion of the photosynthates is characteristic of arctic meadow monocots, irrespective of their latitudinal location. Energy stored in belowground sinks was more efficiently retained within the meadow ecosystem since roots were longer lived than tillers and the stored energy could be used throughout the tiller system.

The wet sedge-moss meadows were ecologically the most suitable growth habitat for Carex stans the dominant lowland meadow species. The average belowground production of these meadows was 129 g/m^2, even though their belowground biomass was 15% less than that of the hummocky sedge-moss meadows. The lowest belowground production of 56 g/m^2 was found in the frost-boil meadow. The low production in large part was due to the limited (51%) intensive areas of plant growth.

Table 24. Maximum belowground total vascular plant standing crops (g/m^2) in tundra communities of other regions, comparable to those of the lowland sedge-moss meadows

Location	Community	Standing Crop (g/m^2)	Reference Source
Truelove Lowland, Devon Island, N.W.T.	Frost-boil meadow	651	
	Hummocky meadow	1633	
	Wet meadow	1367	
Barrow, Alaska	Meadow tundra	1520-2185	Dennis and Johnson (1970)
	Meadow tundra	1075-1600	Tieszen (1970)
Dempster Highway, Yukon	Cotton grass tussock dwarf-shrub heath	2372	Wein and Bliss (1974)
Western Taimyr, U.S.S.R	Spotted tundra	1475	Khodachek (1969)
	Polygonal tundra	2701	
	Hummocky tundra	3474	
	Spotted sedge tundra	1631	Vassiljevskaya and Grishna (1972)
	Marshy tundra	2461	
Yamal-Nenetz district, U.S.S.R.	Swampy meadow	2840	Gorchakovsky and Andreyashkina (1972)

Frost-boils were extremely poor root habitats and possessed approximately 20% of the belowground biomass found beneath the heavily vegetated portions of the meadow. On a totally vegetated basis, the frost-boil meadow production would have been comparable to that of the other meadow community types.

The type of soil found in a meadow had an effect on the degree of belowground production. The warmer and better drained Fibric Organo Cryosols of the intensive study (site 1) and rock-base (site 4) hummocky meadows resulted in their belowground production being 40 - 55% higher than that of the coastal (site 7) hummocky meadow with a Gleysolic Static Cryosol. Although the plateau-base (site 10) also had a gleysolic soil, its more pronounced aboveground growth insured a greater belowground production, one comparable to that of the two former hummocky meadows.

Annual increment of the belowground biomass was approximately 5% of the total standing crop. Such a low annual production indicated that increased root longevity in part helped to offset slow root growth. This would aid in plant energy conservation since less of the energy reserves would be used for new root tissue production and existing roots would be used more effectively over a longer period of time.

Previously reported lowland belowground production rates (Muc 1973) were approximately 25 - 90% higher than those reported here. The former production estimates were based on seasonal total belowground biomass differences and these

required extrapolations of early season belowground standing crops. Computer simulations of meadow belowground production (Whitfield and Goodwin 1976), based on available sedge photosynthetic rate and green tissue biomass data, indicated that those original production estimates were considerably higher than might be expected. The statistical approach to calculating belowground production as a ratio of aboveground: belowground production provided a closer fit between computer predicted and calculated root production. Arkay (1972) had used a similar ratio approach to estimating production on Cornwallis Island but had assumed an equivalent ratio.

Seasonal belowground accretion in comparable low arctic communities of other regions were only slightly higher than those of the lowland meadows. This would have developed from the denser plant growth and more optimal environments found at the more southern latitudes. At Barrow, Dennis and Johnson (1970) reported belowground production to range from 90 - 258 g/m^2 and to represent an annual increment of 17% of the total biomass. In the Western Taimyr Vassiljevskaya and Grishna (1972) reported production as being 114 g/m^2 in a spotty sedge tundra and 165 g/m^2 in a marshy tundra. These represented an average biomass increment of 7%.

Belowground meadow productivity increased along an increasing moisture gradient (frost-boil to wet meadow). Wet meadow productivity averaged 2.51 g/m^2/day and was only 1.16 g/m^2/day at the frost-boil meadow. Similarily productivity was highest in a later and cooler season such as 1972.

This indicated that meadow root growth was not limited by such growth conditions. Low soil temperatures do not appear to restrict root growth of arctic meadow monocots (Billings et al. 1973). Root growth would however be expected to decrease in proportion to the lowering of soil temperatures at lower soil depths.

In Eurasian meadow communities Vassiljevskaya and Grishna (1972) reported belowground productivity as 0.90 - 2.43 $g/m^2/day$, a rate comparable to that of the lowland meadows.

The 24% increment in the root weight of the Carex stans tiller transplants reflected the optimal root growth habitat to be found in the upper soil profile. The increment may over-represent the actual root growth of the sedges since the majority of attatched roots were alive and little of the attatched biomass included dead roots. Furthermore, the attatched roots in the immediate vicinity of the tiller may have possessed greater growth capacities. The process of transplantation must also be considered as being potentially influential in the measured growth rate. Temperate grassland studies have shown that transplanting tillers may stimulate root growth by as much as 20% (Weaver and Zinke 1946) to 100% (Smith 1969). A more realistic approximation of sedge root growth in the upper soil profile, might be on the order of 12 - 20%. Root increments at lower depths would be expected to be considerably lower.

Of the total root increment found in the sedge tiller

transplants, 80% consisted of new laterals and primaries and 20% in the elongation of older roots. New roots would be more efficient in water and nutrient uptake while the old roots would serve as energy sinks and primordia for new root growth.

Meadow Totals

1. Biomass.

Increased vascular plant and non-vascular (moss, algae and lichen) plant biomass content of the lowland plant communities followed an increasing habitat moisture gradient from the raised beach to the sedge meadows (Fig. 35). Mosses contributed approximately 50% of the biomass in the wetter meadow sites. Sedge-moss meadows had 85 - 410% more total vascular plant biomass than did any other lowland plant communities. This was in large part due to their more extensive vegetation cover and pronounced concentration of biomass belowground. Even in the frost-boil meadow where only 51% of the surface area was covered by dense plant growth, had 85 - 160% more total vascular plant biomass than did the non-meadow communities.

Excessively high soil moisture levels (flooded) such as those in the wet meadows, reduced total community vascular plant biomass by approximately 15% in comparison to the more mesic habitats of the hummocky meadows. In these latter meadows developed greater species diversities and higher stem densities. The wet meadows were a more optimal growth habitat for mosses. On a total vascular and non-vascular

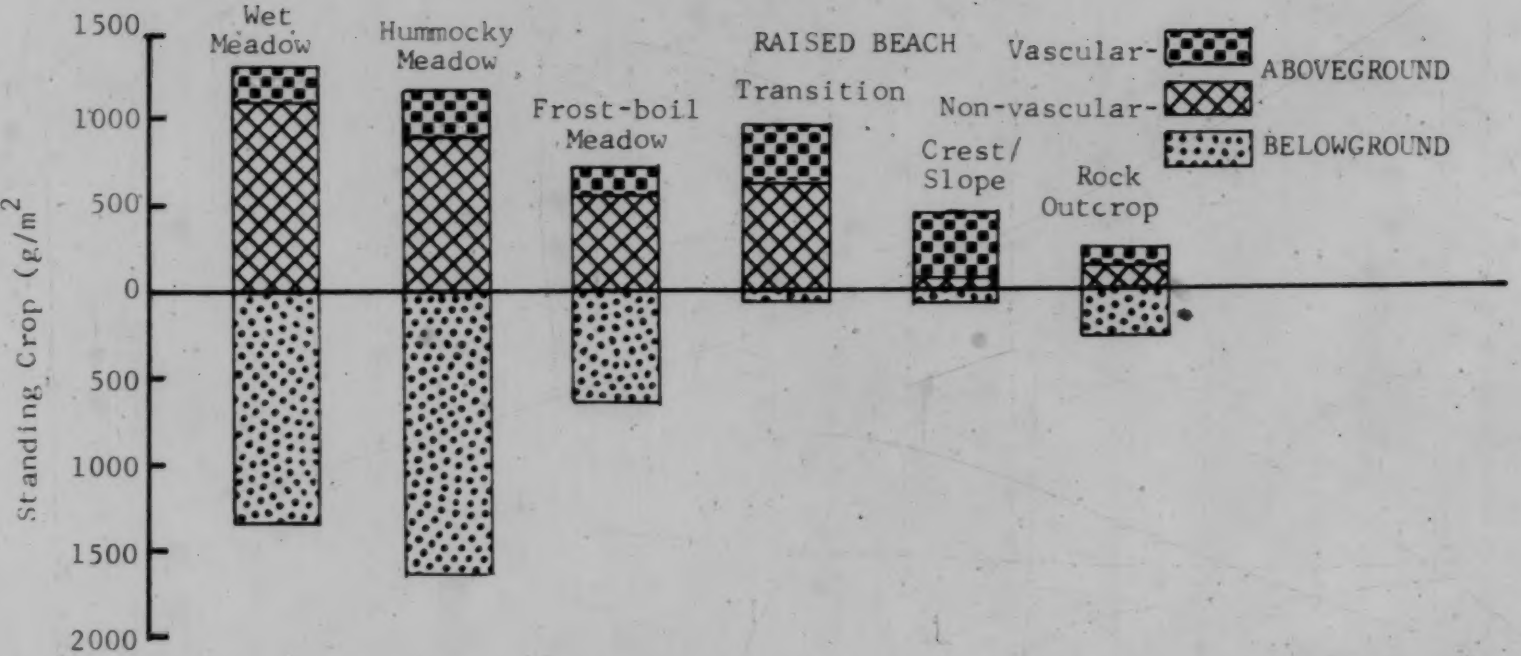

Figure 35. Peak season aboveground and belowground vascular and non-vascular plant standing crops (g/m^2) in the major lowland plant communities. Based on 1 - 4 yrs data (modified from Bliss 1975).

(moss and algae predominantly) basis, standing crops in both the hummocky and wet meadows were similar at 2798 g/m^2 and 2668 g/m^2, respectively. On a total vegetated basis the total biomass of the frost-boil meadow would also have been comparable to those of the other two meadow types.

Belowground standing crops in the lowland communities tended to reflect the community species composition. Monocots of the wetter meadow habitats concentrated the major portion of their biomass belowground while cushion plants (forbs and woody plants) of the drier raised beaches concentrated their main biomass aboveground.

Average peak season aboveground:belowground vascular plant biomass ratios of the lowland meadows ranged from 1:3.8 in the frost-boil meadow to 1:6.7 in the wet meadow. Comparable rock outcrop dwarf shrub-heath community ratios ranged from 1:2.4 - 1:2.9 (Bliss and Kerik 1973). Raised beach cushion plant communities (Svoboda 1973) had ratios of 3.2:1 - 6.0:1.

In comparable Eurasian high arctic meadow sites on Bol'shoj Ljakhovskig Island USSR, Aleksandrova (1970b) reported ratios of 1:5.3 - 1:7.2. At Barrow, Dennis and Johnson (1970) reported considerably higher ratios of from 1:5.9 - 1:17.8 and Tieszen (1970) found similar ratios of 1:11 - 1:14. The higher ratios of these low arctic meadows are attributed to their denser vegetation and corresponding higher belowground biomasses.

2. Net production and productivity.

The vascular and non-vascular (moss, algae and lichen) plant production of the lowland communities increased with an increasing habitat moisture gradient (Fig. 36) as had the community biomass. Total vascular plant production was on the average only 19 g/m^2 on the raised beach and 174 g/m^2 in the wet meadow. In the lowland meadows, the lowest production was found in the relatively 'dry' (moist) frost-boil meadow with 87 g/m^2.

Lowland meadow productivity was 80 - 630% higher than that of non-meadow communities. Raised beach total productivity ranged from 0.34 - 0.38 g/m^2/day (Svoboda 1973) and based on a 50 day growing season, was ca. 0.69 g/m^2/day in the rock outcrops (Bliss 1975). The significant difference in the productivities of the lowland communities is attributed to the productive capacities of the dominant community species. The more productive monocots, dominating lowland sedge-moss meadows, are primarily responsible for the higher productivity of these communities. The cushion plants (forbs and woody plants) did not appear to have such high productive capacities.

Average total meadow productivity ranged from 1.70 g/m^2/day in the frost-boil meadow to 3.39 g/m^2/day in the wet meadow. Interestingly, meadow productivity was highest in a later and cooler (shorter) growing season (1972) than in an earlier and warmer (longer) growing season such as 1971. This might suggest that meadow plant growth is biologically

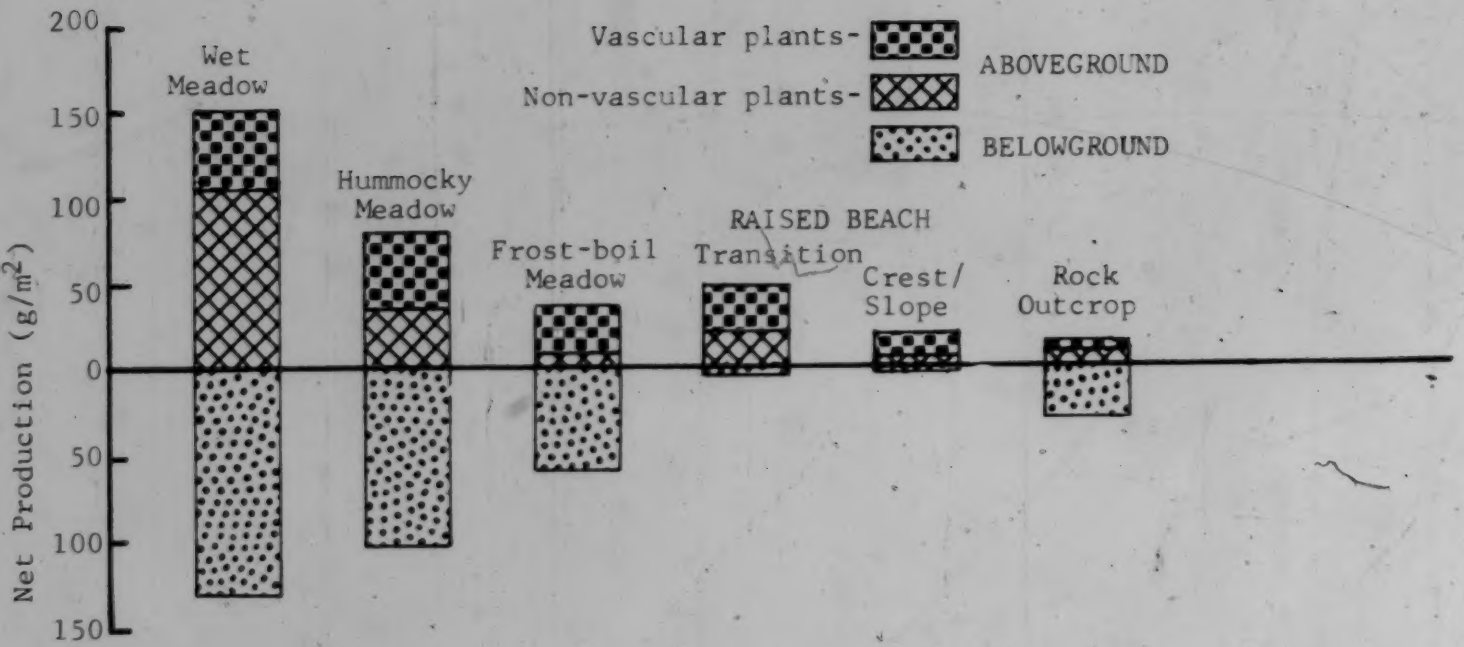

Figure 36. Net primary aboveground and belowground production (g/m^2) of vascular and non-vascular plants in the major lowland plant communities. Based on 1 - 4 yrs data (modified from Bliss 1975).

regulated and develops its maximum growth regardless of the type of growing season experienced. In such a situation, productivity would be highest in the shorter season and lowest in the longest season.

Although the lowland meadows maintained the majority of their biomass belowground, they nevertheless did provide a large available food supply for the lowland's fauna. Grazing in the meadows was however minimal (1 - 2%) due to the wettness of these habitats. Muskoxen were the major meadow herbivore and unlike the situation in low arctic meadows, lemmings did not make a significant grazing impact on the lowland meadows.

Lowland Meadows

In the lowland sedge-moss meadow communities vascular plant standing crops and production increased along an increasing habitat moisture gradient (frost-boil to wet meadow). Lower production and biomass levels in the frost-boil meadow were due to their extensive (49%) areas of low vegetation cover. On a totally vegetated basis their totals would have been as great as those in the two other meadow types. The high productive capacity of the wet meadow type was due to its relatively monospecific (Carex stans) plant composition and an optimal sedge growth habitat. Hummocky meadow biomass and production was also relatively high and developed from their possessing optimal growth habitats for both monocots (hollows) and forb and woody plants (hummocks).

In the overall lowland ecosystem, the sedge-moss meadows

were not only the most prominent plant community but were also its most productive unit. Their extensive development (area) in the lowland must be considered one of the prime factors responsible for the lowland's extensive faunal diversity and biomass.

LITTER AND ORGANIC MATTER

Litter and soil organic matter are important components in a tundra meadow's total nutrient budget (Bunnell 1972, Whitfield 1976). Aboveground and belowground decomposition rates in the lowland sedge-moss meadows are low (Widden 1976)as a result of low soil temperatures, high soil moisture content, and low soil oxygen tensions. The net result is an accumulation of organic materials in the meadow soils. Tundra decomposition processes do function at low temperatures (Flanagan 1971) but would presumably require a longer time interval to be as effective as those of temperate regions.

Seasonal litter collections in the lowland meadows provided an estimate of the availability of aboveground tissue for decomposition as well as the weight attrition of this plant component. Estimates of the organic matter content of lowland meadows provided an insight into its development as well as an indication of potential nutrient reserves.

Methods

Litter

During each growing season, aboveground litter (here used as unattached vascular plant material lying on the moss surface) was carefully collected from each of the plots harvested for primary production estimates. Sampling intensity and frequency have been described in the section on primary production methodology. The litter collected in each sample was not sorted into its constituent plant groups. Determination of litter composition was based on a separate subsnow surface collection of litter at the hummocky intensive study (site 1) meadow. Each of the ten 20X50 cm samples collected was identified as being of hummock and hollow origin. The litter was sorted into monocots, forbs, woody plants, and mosses; oven dried at 85° C for 24 hr; and weighed to an accuracy of 0.1 grams.

Spring meltwater redistribution and potential removal of meadow litter was studied at the hummocky intensive study (site 1) meadow in 1972 (6 - 11 July) and in 1973 (18 - 26 June). Water-borne litter was collected from rivulets by means of 25 litter traps (Fig. 37). Each trap was 20X10 cm in size and consisted of 1 mm^2 plastic mesh. The traps were secured to the frozen ground with nails and had a collection aperature of 15 cm width. Traps were cleared of all the litter collected over a 24 hr period and retained in a rivulet until its water flow ceased completely. Discontinuities in rivulet flow patterns made it impossible to

Figure 37. Litter traps (left foreground and background) used in collecting spring meltwater transported litter, at the hummocky intensive study (site 1) meadow 1972.

calculate the meadow surface area over which litter was being collected and redistributed. The potential collection area of a single litter trap was estimated to be 1 - 3m^2. A 1974 estimate of potential litter removal from the meadow site was made by Ryden (pers. comm.). The single water outlet channel (west side) from the meadow, was monitored with a collection trap and only the total litter collected over the spring melt period was measured.

Organic Matter

Sedge-moss meadow soil organic matter measurements were based on a single harvest period (August 1972). Soils were analysed from the hummocky (site 1), frost-boil (site 13), and wet (site 18) meadows. Collections of screened (1 mm^2 mesh) root core washings (see belowground production methodology) provided the data on soil organic matter content.

Results

Litter

Peak meadow litter standing crops were measured immediately after snowmelt and ranged from an average low of 6 g/m^2 at the wet (site 18) meadow to a high of 12 g/m^2 at the hummocky (site 1) meadow (Table 25). Meadow litter content dropped to 3 - 5 g/m^2, respectively, by mid-August. Seasonal litter weight attrition was on the order of 50% of the peak seasonal weight and occurred at a relatively uniform rate over the growing season. Limited late season (September) litter data indicated little weight loss since August. The major portion of the litter standing crop appeared to form

Table 25. Average (±standard error) monthly litter standing crops (g/m^2) in a frost-boil (site 13), hummocky (site 1), and wet (site 18) sedge-moss meadow (n=6 - 16) 1970 - 1972.

Site	Season	Month			
		June*	July	August	September
13	1971	7.9±1.3	4.4±0.8	2.5±0.4	_____
	1972	9.8±1.3	6.1±0.6	4.4±0.9	_____
	Mean	8.9	5.3	3.5	_____
1	1970	9.6±1.9	5.6±1.8	4.0±1.6	_____
	1971	14.6±2.5	10.9±2.3	4.1±0.7	3.3±0.7
	1972	10.9±1.7	7.3±0.9	6.7±1.3	_____
	Mean	11.7	7.9	4.9	3.3
18	1971	6.4±1.1	3.0±0.4	2.3±0.4	_____
	1972	5.8±1.1	5.0±1.5	3.2±1.2	_____
	Mean	6.1	4.0	2.8	_____

over winter through compaction of the dead foliage and during the spring when freeze/thaw conditions would make the compacted plant material susceptible to breakage.

The majority (49%) of the hummock litter was derived from woody plants and the majority (84%) of hollow litter from monocots (Table 26).

Table 26. Plant component analyses of sub snowsurface hummock (n=5) and hollow (n=5) litter samples (g/m^2 ± standard error) from the hummocky intensive study (site 1) meadow 1971.

Habitat	Mean Weight (g/m^2)	Composition (%) Monocot	Forb	Woody Plant	Moss
Hummock*	6.41±1.57	33	15	42	10
Hummock**	12.97±1.27	20	22	53	5
Mean	9.69±1.57	24	20	49	7
Hollow	3.93±1.40	84	6	10	0
Combined	6.87±1.37	38	17	40	5

* *Salix* absent from hummock. ** *Salix* present on hummock.

Total hummock litter biomass was 150% higher than in the hollows. Mosses, not considered to be a 'natural' component of the litter, made up 5 - 7% of the litter weight.

The accumulated litter collection for the spring litter traps averaged 1.7 g/trap for the six-day period in 1972 and 1.2 g/trap over a nine-day period in 1973 (Fig. 38). Both year's litter collections revealed the peak period as coinciding with peak rivulet flow. Litter redistribution based on an area of 3 m^2 was 4% and on an area of 1 m^2

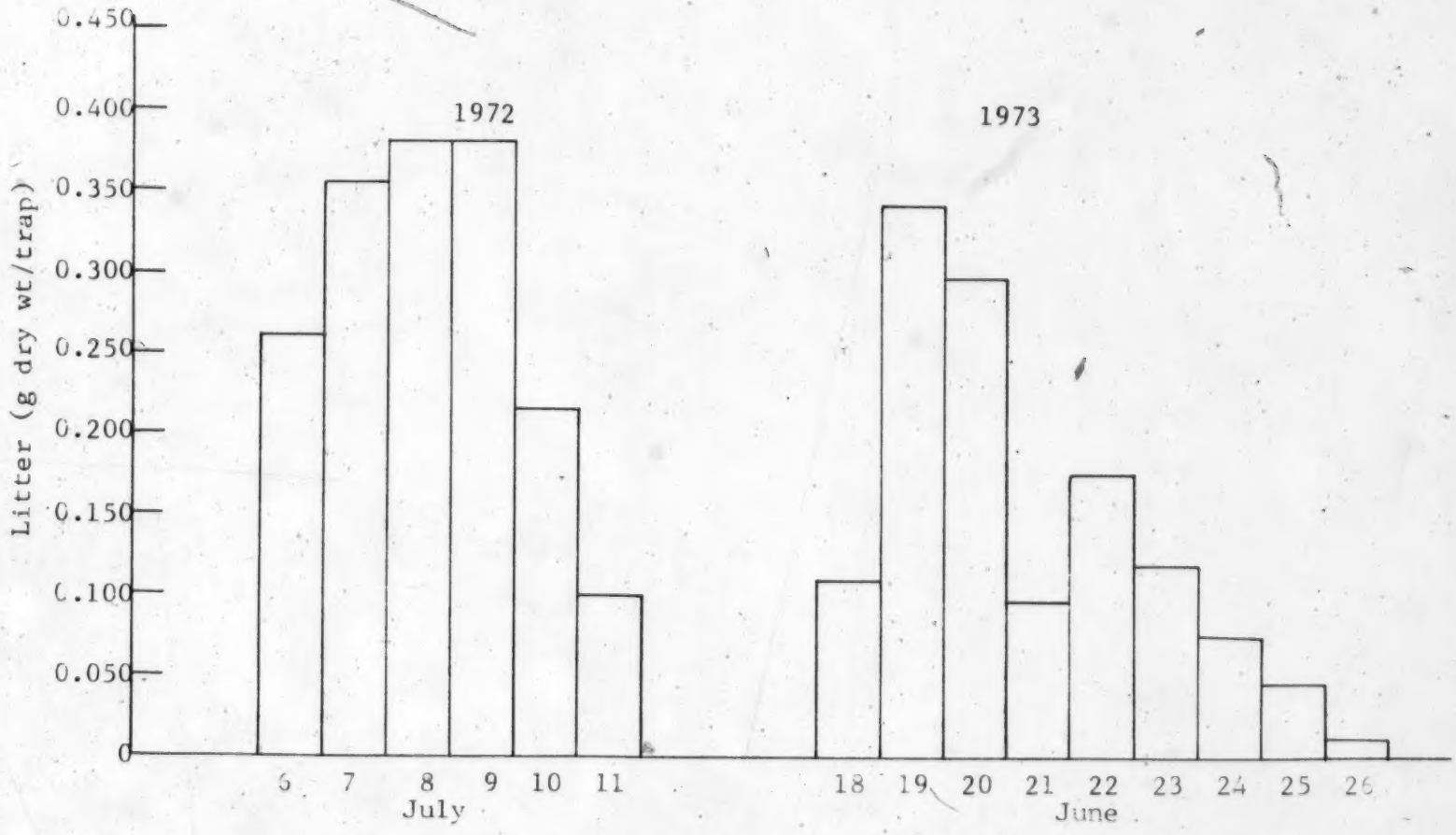

Figure 38. Litter (gram dry weight) collected in individual litter traps (n=25) during the spring melt period at the hummocky intensive study (site 1) meadow 1972, 1973.

was 11%. Meadow litter loss from the community, by way of the stream outlet, was measured as 0.1% of the total litter biomass.

Organic Matter

Soil organic matter conent (23 cm depth) of the hummocky intensive study (site 1) meadow was 28600 g/m^2 and 10400 g/m^2 at the frost-boil (site 13) meadow (Table 27). The wet (site 18) meadow's organic content (26 cm depth) was 13400 g/m^2. Organic content of the mesic Fibric Organo Cryosol (site 1) was 115% higher than in the wetter Fibric Organo Cryosol of the wet meadow and 175% higher than that of the Gleysolic Static Cryosol of the frost-boil meadow. Moss and monocot plant material were the major constituents of the soil organic matter. Maximum depth of organic matter accumulation at the wet meadow was 50 cm and of this, approximately 50% was frozen.

Discussion

Litter

The litter standing crops of the lowland meadows were approximately 20% of the total attached standing vascular plant biomass. These data suggest a five-year turnover rate (attached - litter)for the meadow vegetation. This is identical to the calculated turnover rate based on phenological data. Similar meadow vegetation turnover rates have been reported from low arctic meadows (Dennis and Johnson 1970, Johnson and Kelly 1970). Aleksandrova (1970b) found tundra grass and sedge leaf detachment occurred after

Table 27. Vertical soil organic matter (exclusive of moss and vascular plant material) distribution (g/m^2 and %) in microhabitat soils at the hummocky (site 1), frost-boil (site 13), and wet (site 18) sedge-moss meadows 1972.

Meadow	Depth (cm)	Habitat					
		Hummock		Hollow		Composite	
		g/m^2	%	g/m^2	%	g/m^2	%
Hummocky	0 - 7	5012±813	15	3709±641	15	4373	15
	8 - 15	10756±1318	33	9985±852	42	10378	36
	16 - 23	17233±1272	52	10304±1459	43	13838	49
	Total	33001	100	23998	100	28589	100
Frost-boil	0 - 7	3356±519	17	6034±735	29	2247	21
	8 - 15	12880±1338	63	7496±602	36	5492	53
	16 - 23	4050±688	20	7188±826	35	2693	26
	Total	20286	100	20718	100	10432	100
Wet	0 - 10	1544±194	12			1554	12
	11 - 18	4147±548	31			4147	31
	19 - 26	7675±628	57			7675	57
	Total	13376	100			13376	100

4 - 5 years. A relatively rapid turnover of the aboveground meadow biomass would insure rapid nutrient recycling. This would help to offset the growth limitations imposed by a nutrient limited environment. The low peak litter biomass content (6 g/m^2) of the wet meadow may have resulted from extensive litter removal by fast flowing water streaming through the community during the snowmelt period. Continued submergence of the litter material in water would have contributed to a greater weight loss from leaching. The measured growing season litter weight attrition of 50% was considerably higher than the 15% annual decomposition weight loss measured by Widden (1976). The discrepency in litter weight loss may be explained by an initial overcollection of litter in the late spring. The very wet conditions during this period may have caused the older dead but attached leaf material to lie on the moss and become collected as litter. Morphologically it would not have been identified as litter.

An average peak meadow litter standing crop of 6 - 12 g/m^2 was considerably lower than the 14 - 37 g/m^2 reported (Wielgolaski 1971a) for comparable IBP tundra communities. These lower litter values in the lowland meadows may in large part be attributed to lower meadow biomasses and production, less dense plant growth, a lower plant canopy, and a predominately monocot composition to the meadow vegetation.

Microhabitat characteristics have a definite influence on a meadow's litter content and a larger surface area cover by hummocks would contribute to an increase in the community

litter content. Hummock dwelling forbs and woody plants are deciduous and have an annual leaf turnover. Hollow monocots are also deciduous but their dead foliage remains attached for a number of years.

Although litter is partially (4 - 11%) redistributed within the meadow complex, little (0.1%) of it is actually removed from the community. Litter samples showed less than 1% of the plant material as being green, indicating that in the sampled meadows grazing did not make a significant contribution to the litter component. Grazing is however an important factor in the litter component of more intensively grazed meadows (Hubert 1976). Snow compaction and spring mechanical breakage of dead tissue appeared to be the most significant meadow factors in the formation of litter.

Organic Matter

Meadow soil organic matter content ranged from 10400 - 28600 g/m^2. Moss and vascular plant tissue would have contributed an additional 15 %. In a low arctic sedge meadow Haag (1974) found soil organic matter content to total 23000 g/m^2. Comparable Eurasian tundra meadow sites had 24400 - 29500 g/m^2 (Vassiljevskaya and Grishna 1972). Annual peat accumulation in the lowland meadows would be of primarily moss material in the upper 5 cm of the soil and of vascular plant material in the lower soil profile. Soil peat content increased with depth as a result of compaction. Accumulation of organic matter in the lowland meadows was influenced by low soil temperatures and high soil moisture levels, both of

which contributed to a reduction in organic matter decomposition. Annual peat accumulation at the wet (site 18) meadow was calculated to be 6 - 8 g/m^2 and Pakarinen and Vitt (1973b) had calculated it as being less than 10 g/m^2 for the lowland meadow communities. The Fibric Organo Cryosol soils have extensive peat accumulation throughout their profiles, while the Gleysolic Static Cryosols have it concentrated in the upper 15 - 25 cm of their profile. No buried organic layers were found in the lower mineral portions of these latter soils. This would suggest that the development of a vegetation canopy has proceeded without major disruptions. The most abundant biomass and production was generally associated with meadows possessing Fibric Organo Cryosols.

PLANT CANOPY

Chlorophyll content of arctic monocots is higher than in comparable alpine species (Tieszen and Bonde 1967). Similarily comparative photosynthetic capacities of Oxyria digyna are higher in arctic plants than they are in alpine plants (Billings et al. 1971). The shortness of the arctic growing season (ca. two months) has necessitated more efficient photosynthesis and a greater synchrony between community chlorophyll and biomass content. Such high correlations between community chlorophyll and biomass have been found in low arctic meadows (Tieszen 1972b Dennis and Tieszen 1972).

The plant canopy of arctic meadows provides a characteristically extensive plant cover but is low and poorly (two tier) stratified. Leaves of the meadow species are generally thin and more than 50% of the foliage is located in the lower 5 cm of the canopy (Tieszen 1970). The lack of any pronounced canopy stratification is evidenced in the low leaf area indices reported for arctic meadow communities (Dennis and Tieszen 1972, Muc 1973). Meadow plants are extremely efficient in intercepting incoming radiation and only a small portion of the radiation reaches the ground surface (Tieszen 1970, Addison 1976). The success of arctic meadow communities is in large part due to their efficient utilization of incoming radiation.

Comparative plant canopy studies within the lowland meadows concentrated on community and species chlorophyll content, community photosynthetic leaf area indices, and species leaf orientation. The majority of these studies focused on Carex stans , the dominant meadow vascular species.

Methods

Chlorophyll

During the 1971 growing season tissue chlorophyll determinations were made on a community (mg/m^2) and species (mg/g dry photosynthetic tissue weight) basis for Carex stans, C. membranacea, C. misandra, Eriophorum angustifolium, E. triste, Arctagrostis latifolia, Polygonum viviparum, and Salix arctica. Sampling was carried out at the hummocky (site 1), frost-boil (site 13), and wet (site 18) meadows and

consisted of weekly triplicate 20X50 cm aboveground samples collected within staked 4X8 meter plots at each meadow. In 1972, tissue chlorophyll content was only determined for Carex stans and weekly sampling consisted of triplicate collections of ten plants each from a hummock and hollow habitat at the hummocky and forst-boil meadows and from a submerged and emergant habitat at the wet meadow. Chlorophyll measurements of Carex stans from the greenhouse consisted of harvesting 25 sedge tillers at the peak of the growing season (mid-August).

The harvested shoot material was sorted by species into live and dead components. One gram of photosynthetic tissue was used for the chlorophyll extraction and the remaining green leaf material was weighed fresh and pressed for subsequent tissue moisture (%) and leaf area (cm^2/g dry wt) determinations. The chlorophyll sample was ground up with a mortor and pestle; chlorophyll extracted with 50 cc of 80% acetone for 24 hr; and the extract filtered through Whatman #1 filter paper. Degradation of tissue chlorophyll by plant acids, light, and heat (Zscheile and Comar 1941) was kept at a minimum by using alkaline ($MgCO_3$) acetone and making all colorimetric analyses under subdued light conditions. The extract chlorophyll content (Δ optical density) was read at wavelengths of 645 mμ and 663 mμ on a Spectronic 20 (Bausch and Lomb) colorimeter. Chlorophyll content was calculated on the basis of Arnon's (1949) formula:

$$C_{a+b}\ (mg/l) = 20.2 \times OD_{645} + 8.02 \times OD_{663}$$

Chlorophyll content was then recalculated on a tissue weight basis.

Leaf Area Index

Photosynthetic leaf area measurements were taken on the tissue remaining from the chlorophyll analyses. A photoelectric planimeter, similar to the one described by Donovan et al. (1958). Green leaf area measurements were made on 25 Carex stans tillers, taken from the greenhouse at the peak of the growing season (mid-August) in 1972. Accuracy checks of the photoelectric leaf area determinations were made with graph paper measurements of monocot, forb, and woody plant leaf samples (n=20). Both sets of area measurements were identical for forb and woody plant leaves but monocot leaf areas were being photoelectrically underestimated by 15%. This measurement error arose from leaf overlap. All photometric monocot measurements were corrected accordingly and all leaf areas (two sides) expressed on a community basis. Leaf area index = LAI.

Leaf Display

Leaf inclination angle measurements (1972) were taken exclusively from Carex stans tillers on hummocks and in hollows at the hummocky intensive study (site 1) meadow. In each weekly sampling (n=3) all attached leaves ($n_{\bar{X}} = 13$) of ten tillers, from each of the microhabitats, were identified as being totally dead, partially photosynthetic, or totally photosynthetic. Angles of orientation from the horizontal were taken for each leaf (Fig. 39).

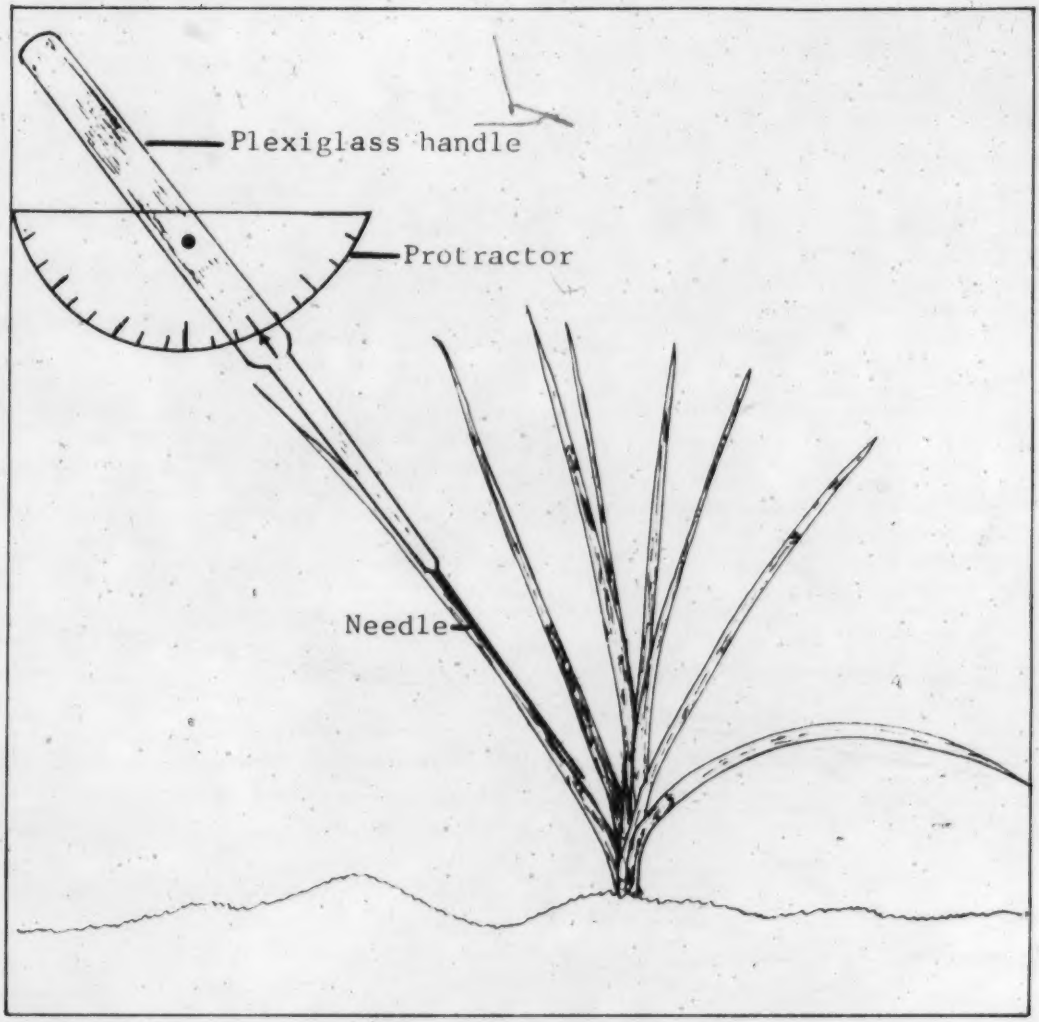

Figure 39. Instrument used in measuring the sedge leaf angles (after Ondok 1973).

Results

Chlorophyll

In 1971, less than 10% of the chlorophyll contained in the overwintering green monocot tissue (Fig. 40) was found to show post-snowmelt deterioration. Rapid monocot chlorophyll synthesis was initiated immediately after meadow snowmelt but a similar development in the forbs and woody plants was not measureable until early July, approximately two weeks later. High community chlorophyll levels were maintained in the three meadow community types through late July and early August, dropping sharply by mid-August. Peak community chlorophyll content was 162 mg/m^2 at the frost-boil (site 13) meadow, 262 mg/m^2 at the hummocky (site 1) meadow and 283 mg/m^2 at the wet (site 18) meadow. Monocots contributed 85 - 90% of the community chlorophyll at the frost-boil and hummocky meadow and approximately 95% at the wet meadow. The seasonal (1971) pattern of community chlorophyll content and green shoot biomass (Fig. 34) showed a similar seasonal development. Correlation of community chlorophyll and photosynthetic leaf area index proved insignificant ($r=0.59$).

Overwintering green monocot tissue retained 3.8 mg/g of chlorophyll. The peak tissue chlorophyll content of Carex stans was 9.3 mg/g at the frost-boil (site 13) meadow, 8.0 mg/g at the hummocky (site 1) meadow, and 8.3 mg/g at the wet (site 18) meadow. Peak tissue chlorophyll content of Salix arctica was 6.4 mg/g at the frost-boil meadow and 7.3 mg/g at the hummocky meadow. Comparable Polygonum viviparum

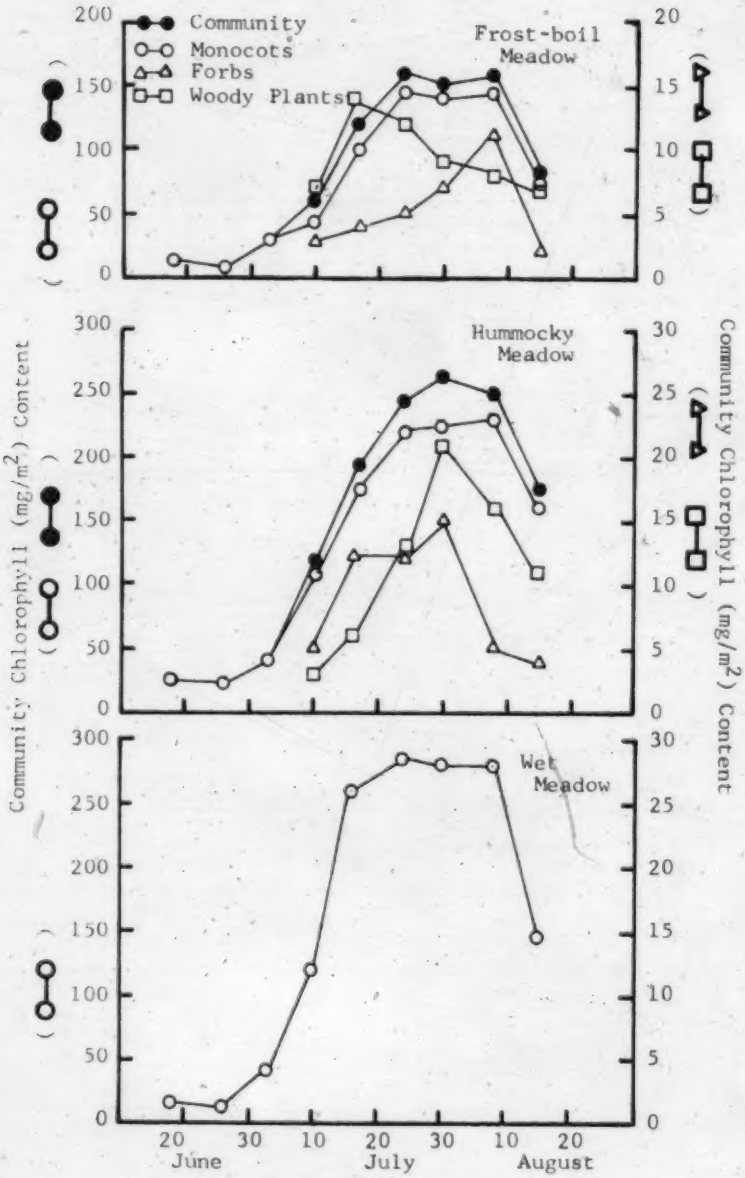

Figure 40. Plant group contribution to community chlorophyll content in a frost-boil (site 13), hummocky (site 1), and wet (site 18) meadow 1971.

chlorophyll content in these two meadows was 10.4 and 11.1 mg/g, respectively. Tissue chlorophyll a:b ratios in all three meadows ranged from 1.1:1 - 1.5:1 and showed no pronounced variability over the season or from site to site.

Carex stans tillers growing in hollows and submerged habitats maintained slightly higher (1 - 2 mg/g) tissue chlorophyll levels than did tillers in the hummock and emergent habitats (Fig. 41). Maximum tissue chlorophyll peaks in all three meadows and in all habitats, were reached by early August (1972). Overall Carex stans chlorophyll content was highest in the frost-boil meadow and lowest in the wet meadow. In the field greenhouse at the hummocky intensive study (site 1) meadow, peak Carex stans leaf chlorophyll levels were 22 - 32% higher than those of the controls.

Leaf Area Index

Photosynthetic leaf area indices in all three meadow communities had a relatively linear seasonal increment. Peak community photosynthetic leaf area indices developed by early August and were 0.31 at the frost-boil(site 13) meadow, 0.38 at the wet (site 18) meadow, and 0.63 at the hummocky (site 1) meadow. Individual Carex stans tillers had photosynthetic leaf areas of 8 cm^2 in the wet meadow, 7 cm^2 in the hummocky meadow and 4 cm^2 in the frost-boil meadow (Fig. 42). Hummock habitats appeared to favor greater tiller leaf areas. Carex stans photosynthetic leaf areas, in the field greenhouses, were 23 - 36% greater than those of the controls.

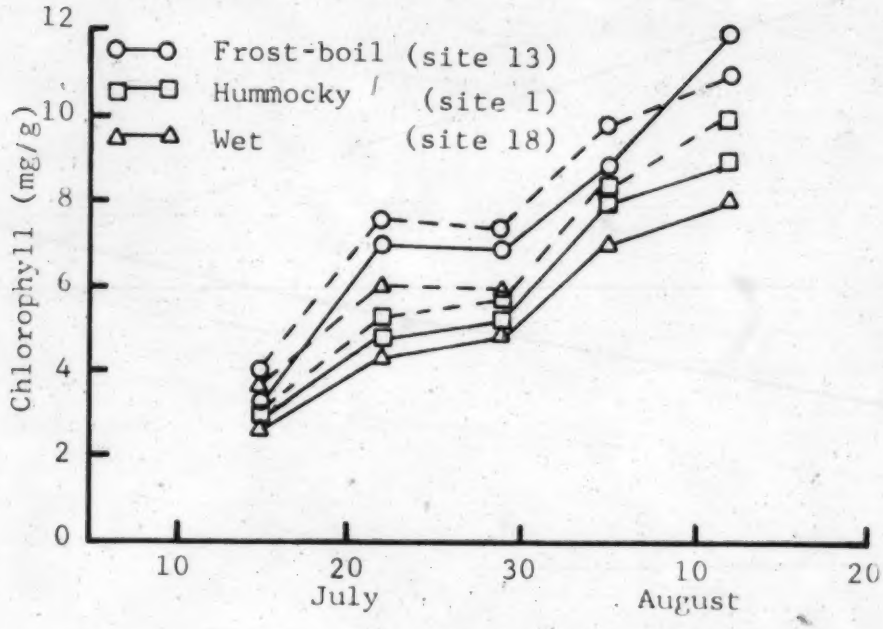

Figure 41. Seasonal Carex stans tissue chlorophyll content (mg/g dry wt) from hummock (solid) and hollow (broken) habitats at sites 1 and 13 and from a submerged (broken) and emergent (solid) habitat at site 18 1972.

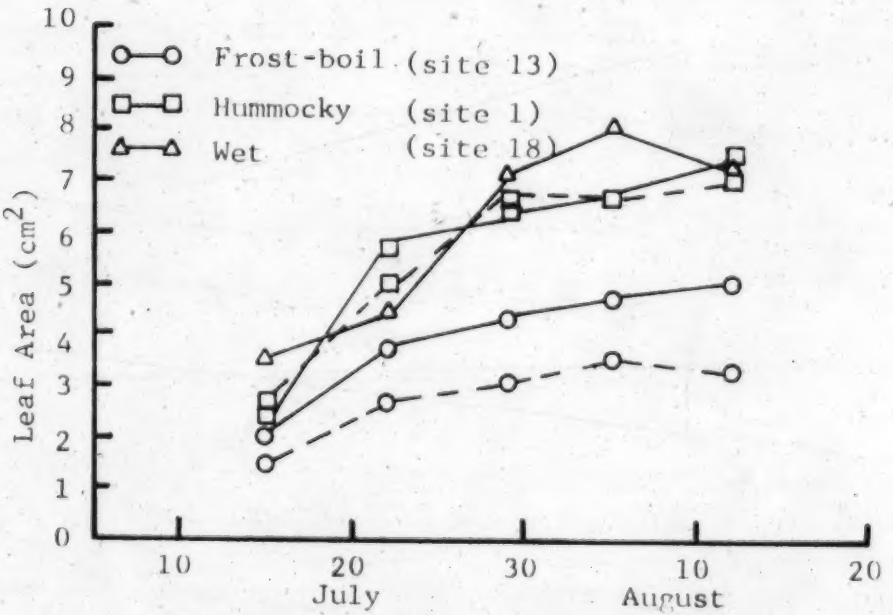

Figure 42. Individual Carex stans tiller photosynthetic leaf areas (cm^2) in hummock (solid) and hollow (broken) habitats at sites 1 and 13 and in emergent habitats at site 18 1972.

Leaf Display

Attached leaves on a Carex stans tiller had angles of orientation proportional to their phenological stage of development (Fig. 43). Totally photosynthetic leaves were displayed at an angle of 75° - 80°; partially photosynthetic leaves at 60° - 70°; and totally dead leaves at 30° - 40° in hummock habitats and at 10° in hollow habitats. The angle of leaf orientation remained fairly constant over the course of the growing season. An average Carex stans tiller growing on a hummock had 26% of its leaves displayed at angles of 75° - 90°; 30% at angles of 60° - 75°; and 44% at angles of 0° - 60°. A comparable composition of leaf display in tillers growing in hollows were 20, 29, and 51%, respectively.

The average vascular plant canopy height of the lowland meadows was less than 10 cm. Monocots dominated the upper 5 - 10 cm of the canopy and constituted 82% of the total vascular plant cover. Forbs and woody plants dominated the lower 5 cm of the canopy and contributed 10 and 8%, respectively, of the plant cover.

Discussion

Chlorophyll

Peak community chlorophyll levels of 161 - 283 mg/m^2, in the lowland meadows, were considerably lower than the 130 - 760 mg/m^2 reported for low arctic meadows (Tieszen and Johnson 1968). Peak community chlorophyll content in the meadow at Barrow was 458 mg/m^2 and 329 mg/m^2 at Prudhoe Bay,

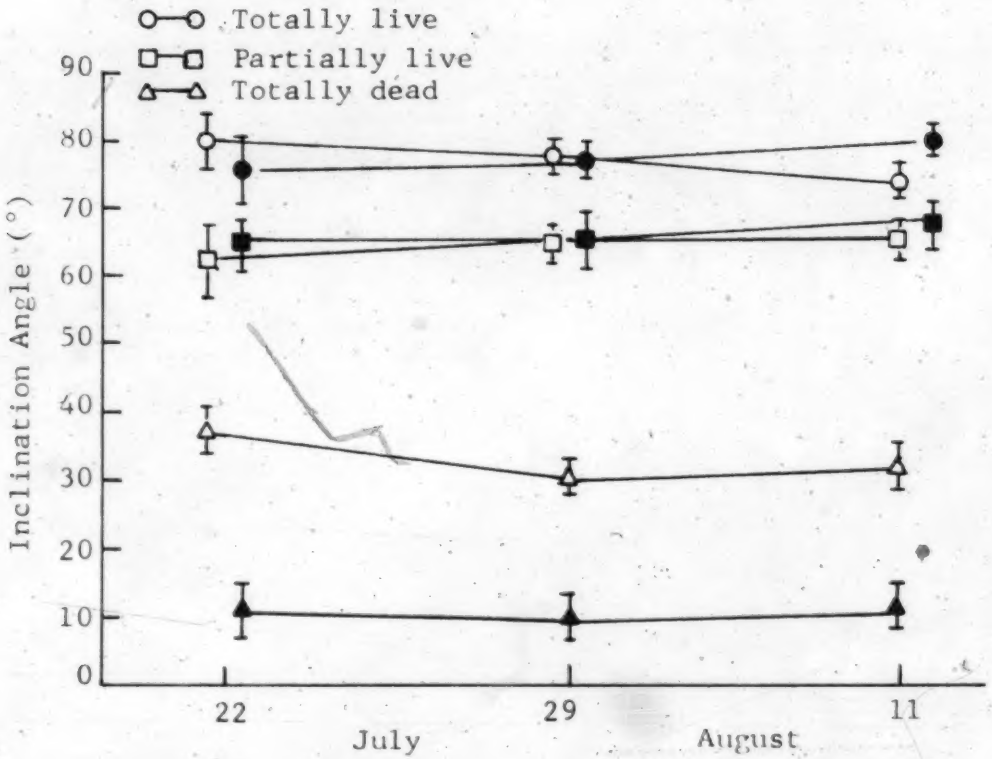

Figure 43. Angles of inclination from the horizontal (standard error) for Carex stans (n=10 tillers) leaves in tillers from a hummock (open) and hollow (closed) habitats at the hummocky intensive study (site 1) meadow 1972.

Alaska (Tieszen 1970). Lower (50 - 75%) stem densities in the lowland meadows would account for the major portion of this difference in community chlorophyll content. Temperature (Friend 1960) and soil nitrogen levels (Haag 1974) are further considerations in understanding community chlorophyll differences. Low (< 10° C) lowland meadow canopy temperatures and low soil nitrogen levels might also have contributed to lower chlorophyll production.

Meadow monocots overwintered with an average chlorophyll content of 20 mg/m^2 and were therefore able to become photosynthetically active at an earlier date than were the forbs and woody plants. Although chlorophyll development in these two latter groups was later in its initiation, it proceeded at a faster rate and peak community forb and woody plant chlorophyll levels were reached by late July. Peak monocot community chlorophyll levels were not found until early August. The forbs and woody plants, occupying the lower half of the plant canopy, had to maximize their foliage chlorophyll content early in the season to counteract the shading effect of monocots later in the season. A similar seasonal sequence of plant group chlorophyll development has also been found (Dennis and Tieszen 1972) in low arctic meadows. The relatively short (one week) interval in the development of plant group chlorophyll peaks correlated with the synchrony found in lowland meadow community chlorophyll and biomas peaks. A decline in the meadow community chlorophyll levels by mid-August coincided with declining incoming radiation

levels and ambient temperatures (Courtin and Labine 1976). Svoboda (1974) found similar developments in the community chlorophyll content of lowland raised beaches.

The 22 - 32% increase in chlorophyll content of greenhouse Carex stans tillers was attributed to the increase (7° C) in canopy temperatures. Such higher temperatures would appear to stimulate greater tissue and subsequently greater chlorophyll, production. Under a raised beach field greenhouse, Svoboda (pers. comm.) found that the tissue chlorophyll levels increased 25 - 100%. Higher tissue chlorophyll concentrations in Carex stans tillers were considered to be adaptations to more stressful habitats. Tillers growing in hollows and submerged habitats, as well as those in the more alkaline soils of the frost-boil meadow, were considered to be growing under environmental stresses. The higher tissue chlorophyll levels would allow these tillers to photosynthesize at rates comparable to those of tillers growing in more optimal microhabitats.

Meadow peak tissue chlorophyll levels of 7.3 - 11.1 mg/g were considerably higher than the 3 - 4 mg/g content of raised beach cushion plants (Svoboda 1973). At Barrow, Dennis and Tieszen (1971) found meadow monocot and forb chlorophyll levels of 5.0 - 7.5 mg/g. The somewhat higher chlorophyll levels of the meadow plants may be used to insure maximum photosynthesis at the lower temperatures found in these communities.

The 3.8 mg/g of chlorophyll concentrated in the over-

wintering green monocot tissue, was associated with the youngest leaves. The majority (90%) of this chlorophyll was retained after snowmelt. At Barrow, Tieszen (1972a) found almost total deterioration (photoxidation?) of this component. Seasonal tissue chlorophyll levels (8.0 - 9.3 mg/g) in Carex stans were considerably higher than those (6.1 mg/g) in C. aquatilis at Barrow. This would suggest that the high arctic monocots have developed the capacity to be more efficient in concentrating and retaining their tissue chlorophyll and in this way be able to maintain photosynthetic rates comparable to those of low arctic monocots. Photosynthetically high arctic C. stans and low arctic C. aquatilis appear to possess similar properties. Mayo et al. (1976) found the light compensation level of lowland C. stans to be 0.01 ly/min and its maximum photosynthetic rates to be 16.8 - 21.0 mg/dm^2/hr. These are similar to the light compensation levels and maximum photosynthetic rates reported (Tieszen 1972c) for low arctic C. aquatilis.

The chlorophyll $_a$ content of meadow plants was higher than that of chlorophyll $_b$. The seasonal chlorophyll $_{a:b}$ ratios of 1.1:1 - 1.5:1 were similar to the 0.9:1 - 1.8:1 found (Svoboda 1974) in raised beach cushion plants. In low arctic meadows, ratios of 1.5:1 - 3.2:1 have been found (Tieszen 1972a). This may be a further ecophysiological response to the latitudinal gradient between low arctic and high arctic meadow environments.

Leaf Area Index

The 0.3 - 0.6 photosynthetic LAI range in the lowland meadows is proportional to meadow stem densities. The hummocky meadow, with stem densities approximately 100% higher than those of either the frost-boil or wet meadow, had a similar 100% increase in community photosynthetic LAI. A similar explanation may be applied to the lower leaf area indices found in high arctic meadows as compared to low arctic meadows. In the lowland raised beach community, the sparse vegetation cover allowed for a leaf area index of only 0.1 (Svoboda 1972). At Barrow, Tieszen (1970) found that the leaf area of dead shoot material was equal to that of the live component. Using this extrapolation for the lowland meadows, would provide a total LAI of 0.6 in the frost-boil (site 13) meadow; 0.8 in the wet (site 18) meadow; and 1.3 in the hummocky (site 1) meadow.

Community chlorophyll and LAI showed a negative correlation but did maintain an overall similarity in their seasonal development. Under greenhouse conditions, photosynthetic leaf areas of Carex stans increased by 23 - 36% and equivalent increments were found for tissue chlorophyll content. The higher (7° C) greenhouse canopy temperatures were considered to be responsible for these increases. Similar greenhouse leaf area increments have been found at Barrow (Tieszen 1970).

The relatively low (< 10 cm) meadow plant canopy height; low (1100 - 2200 stems/m^2) plant density; and low (58 - 86%)

plant cover would contribute to a minimum of inter- and intra-specific plant competition. This would help explain the relatively minor (< 10%) annual variation found in meadow biomass and production. At Barrow, the meadow plant canopy was slightly less than 15 cm high (Caldwell et al. 1972) and stem densities were on the order of 4,800 stems/m^2 (Dennis and Tieszen 1972). Tieszen (1972c) found that the increased leaf shading reduced photosynthetic efficiency in the lower canopy by as much as 58%. Even in the less dense and shorter lowland meadow canopies, most of the incoming radiation was intercepted before it reached the moss surface (Addison 1976). The forbs and woody plants of the lower canopy levels offset and potential shading by monocots through an earlier development of peak tissue chlorophyll levels and maintenance of higher tissue chlorophyll levels.

Leaf Display

Photosynthetically active leaves constituted 49% of the leaf compliment of Carex stans tillers growing in hollows and 56% of the leaf compliment of hummock tillers. By maintaining their angles of display between 60° - 90°, these leaves were more efficient in their interception of incoming solar radiation. At Barrow, meadow monocot leaf display was generally at angles greater than 60° and in Carex aquatilis and Dupontia fisheri were predominantly at 70° - 80° (Caldwell et al. 1972).

Totally dead C. stans leaves were displayed at angles

less than 60° and 50% of such leaves on hollow inhabiting tillers were prostrate on the moss surface. The lower leaf angles and prostration were caused by the wetter conditions of the hollow habitats. The wetter and more extensively leached leaves of hollow tillers were also structurally weaker than their counterparts on hummock tillers. They were therefore more susceptible to being broken off and becoming incorporated into the meadow litter at an earlier stage of their development.

CARBOHYDRATES

Maintenance of high carbohydrate reserves by arctic plants is a major physiological adaptation to survival in such a harsh environment. Plant carbohydrate levels are known (Mooney and Billings 1960) to increase at lower temperatures and under conditions which reduce assimilation. These conditions are characteristic of those under which arctic meadow species grow. Retention of high belowground carbohydrate reserves provides the meadow species with the ability to initiate rapid growth early in the growing season. Carbohydrate accumulations are also involved in the development of frost-hardiness (Parker 1963, Levitt 1960).

The characteristic carbohydrate reserve development in meadow plants consists of an early season depletion of stored reserves; followed by a buildup of carbohydrate reserves in aboveground tissue; and a subsequent late season translocation of these aboveground concentrations into belowground

sinks. The high (85%) concentration of meadow biomass below-ground provides an extensive sink for such reserves. Seasonal carbohydrate cycling in meadow sedges (Carex membranacea and C. stans) was examined on a morphological basis of carbohydrate allocation. Studies were also conducted on the effect of habitat and phenological development on carbohydrate levels in various C. stans tissue.

Methods

Carbohydrate analyses of Carex membranacea (1970) and C. stans (1971) tissue, were based on plant material collected from 20X20 X10 cm deep sod block samples (n=3) extracted from a permanent 4X8 meter plot at the hummocky intensive study (site 1) meadow. Sampling was carried out at three day intervals in 1970 and at six day intervals in 1971. In 1972, the C. stans carbohydrate sampling was taken at irregular (ca. > 1 week) intervals. Analyses of carbohydrate content in phenologically distinctive C. stans tillers were based on only two harvests (June 29, July 20). Inter-meadow C. stans carbohydrate variability was studied at the hummocky (site 1) and wet (site 18) meadows and was based on two (May 15, June 16) harvests.

All the harvested tillers were washed immediately after collection and divided into shoot, rhizome, and tiller components. These components were not further subdivided into live and dead fractions. In the 1972 harvests, the tillers were initially sorted into groups: mature tillers,

mature tillers with a basal tiller bud, young tillers, tiller buds, and flowering tillers. Mature tillers were defined as those with one or more season's attached dead foliage and young tillers as those without any dead foliage. Each group's tillers were then divided into leaf, stem base, rhizome, root, tiller bud, and flower components.

The various tissues were 'fixed' in hot alkaline (Na_2CO_3) 80% ethyl alcohol as described by Fonda and Bliss (1966). In the laboratory, the insoluble tissue ($\leq$ 5g) in each field-prepared sample was filtered out; dried at 80° C for 24 hr; and ground up to pass through a 20 mesh screen. The ground tissue was extracted in a fresh 80% ethyl alcohol solution for 6 hr on a Soxalet extractor. The extracted and original solutions were combined for further analysis. Insoluble dry residues were weighed (0.1 g accuracy) and stored for polysaccharide (starch) analysis.

The alcohol extract solution was purified with lead subacetate (Ward and Johnston 1962); filtered; and brought up to equal volume. The quantity of reducing sugars (monosacchardies) in each sample was determined in duplicate, using Nelson's (1944) arsenomolybdate colorimetric technique. Readings were made, on a Spectronic 20 (Bausch and Lomb) colorimeter, at a wavelength of 600 mμ. This wavelength was found to provide a better sugar claibration curve, for low sugar concentrations, than did the wavelength of 540 mμ used by Fonda and Bliss (1966).

Mild hydrolysis (1 N HCl for 20 min in an 80° C water

bath) of an extract subsample broke down oligosaccharides into monosaccharides. Monosaccharide levels were determined by the procedure described in the previous paragraph. Warren Wilson (1954) found that the monosaccharide difference between unhydrolized and hydrolized samples was an accurate measurement of oligosaccharide content.

Polysaccharide (starch) in the insoluble tissue residues were hydrolized with α- amylase, a substitute for the takadiastase originally used by Ward and Johnston(1962). Monosaccharides were extracted with a fresh 80% ethyl alcohol solution on Soxalet extractors and measured as before.

All of the carbohydrate concnetrations were expressed as mg/g oven dry alcohol-insoluble dry tissue weight. This is the most widely used literature expression of carbohydrate levels in plant tissues. Recently, McCown and Tieszen (1972) have shown that this method of expressing carbohydrate concentrations may result in values 200% higher than those expressed on a mg/g original dry weight basis. Soft tissue breakdown and excessive extraction of cell contents appear responsible for these discrepancies. Using the 1972 samples, 10% of the unpurified extract of 30 Carex stans tissue samples was allowed to evaporate in pre-weighed watch glasses. The dried residues from these samples indicated that 25$\pm$2.6% of the original tissue dry weight had been dissolved in the alcohol. The alcohol-insoluble tissue dry weight (residue) expression of carbohydrate content for the

Carex stans was therefore 25% higher than if it had been expressed on a mg/g original dry weight basis.

Results

Over the course of the growing season Carex membranacea and C. stans tillers showed a trend of depleting their belowground carbohydrate reserves early in the season and rebuilding them toward the end of the season (Fig. 44). Early season shoot total carbohydrate levels were less than 50 mg/g and were 20 - 100% higher in roots and rhizomes. Both sedges maintained seasonal rhizome total carbohydrate reserve levels 25 - 150% higher than those in roots. By mid to peak season, shoot total carbohydrate levels were 80 - 140% higher than those in belowground structures. In both species early season total carbohydrate concentrations were 17% of the total tiller weight and increased to 24% by the peak of the season. In the late stages of the growing season the aboveground:belowground carbohydrate levels were approaching those found in the early part of the season. Inter-tissue translocation of carbohydrates produced the observed seasonal differences in carbohydrate levels.

Post snowmelt Carex stans tiller total carbohydrate levels were approximately 20% higher in 1972, than in 1971. No significant change was found in the carbohydrate content of sedge tillers between mid-May and mid-June but post snowmelt tiller carbohydrate content dropped by 10% (Fig. 45). The carbohydrate regime of sedge tillers was similar in 1971

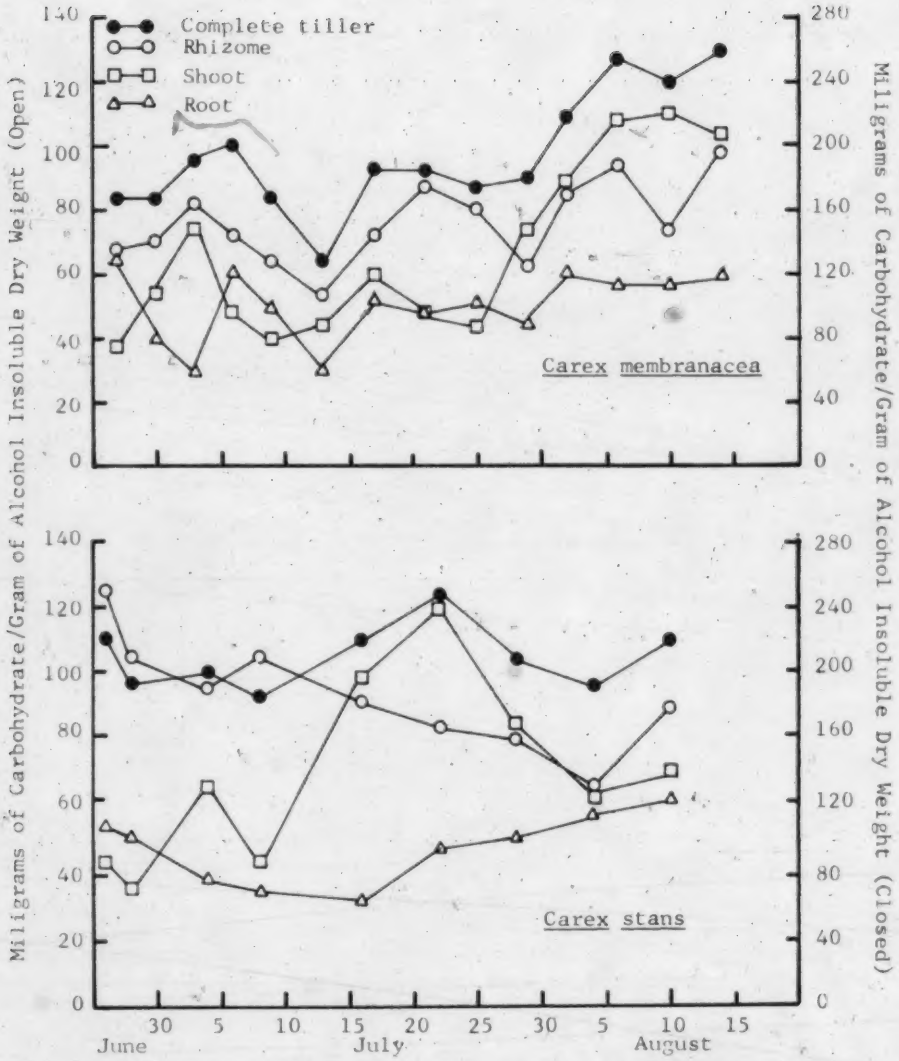

Figure 44. Seasonal changes in carbohydrate content (mg/g alcohol insoluble dry weight) of Carex membranacea (1970) and C. stans (1971).

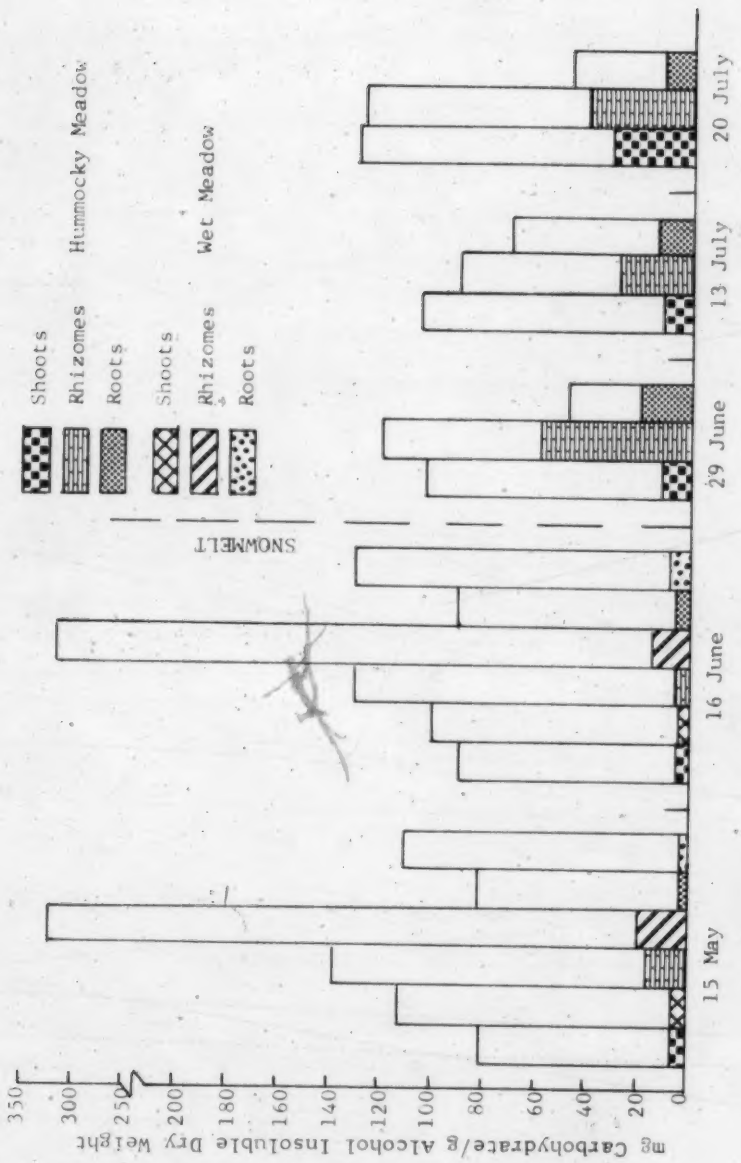

Figure 45. Seasonal changes in monosaccharides plus oligosaccharides (open) and polysaccharides (blocked) content of different Carex stans tissue from a hummocky (site 1) and wet (site 18) sedge-moss meadow 1972.

and 1972. A pre-snowmelt comparison of carbohydrate content in tillers from the wet (site 18) and hummocky (site 1) meadows showed tillers from the latter site to possess carbohydrate levels 40% higher in their shoots and roots and 140% higher in their rhizomes.

The average post-snowmelt sedge starch (polysaccharide) content was less than 10 mg/g. A pronounced and rapid conversion of sugars to starches occurred over the growing season and raised tissue starch levels to 30 mg/g in roots, 60 mg/g in rhizomes, and 20 mg/g in shoots (Fig. 46). Rhizome and root starch levels equalled or surpassed tissue sugar levels by the peak of the season. Average seasonal sugar:starch ratios ranged from 4:1 - 20.5:1 in shoots, 1.2:1 - 2.6:1 in rhizomes, and 2.0:1 - 2.3:1 in roots. Sedge tissue sugars were primarily (98%) of oligosaccharides and showed seasonal oligosaccharide:monosaccharide levels of 12:1 - 29.5:1 in shoots, 24:1 - 77:1 in rhizomes, and 40:1 - 44.6:1 in roots. Shoot monosaccharide levels were approximately 130% higher than those of belowground structures.

Early season mature and mature with basal bud tillers had only slightly (15%) higher shoot carbohydrate levels than were found in young tillers. Their stem base carbohydrate concentrations were however significantly (550 - 665%) higher (Fig. 47). Mature tillers with a bud and young tillers were found to have 160 - 170% more belowground carbohydrate reserves than were found in mature but unreproductive tillers.

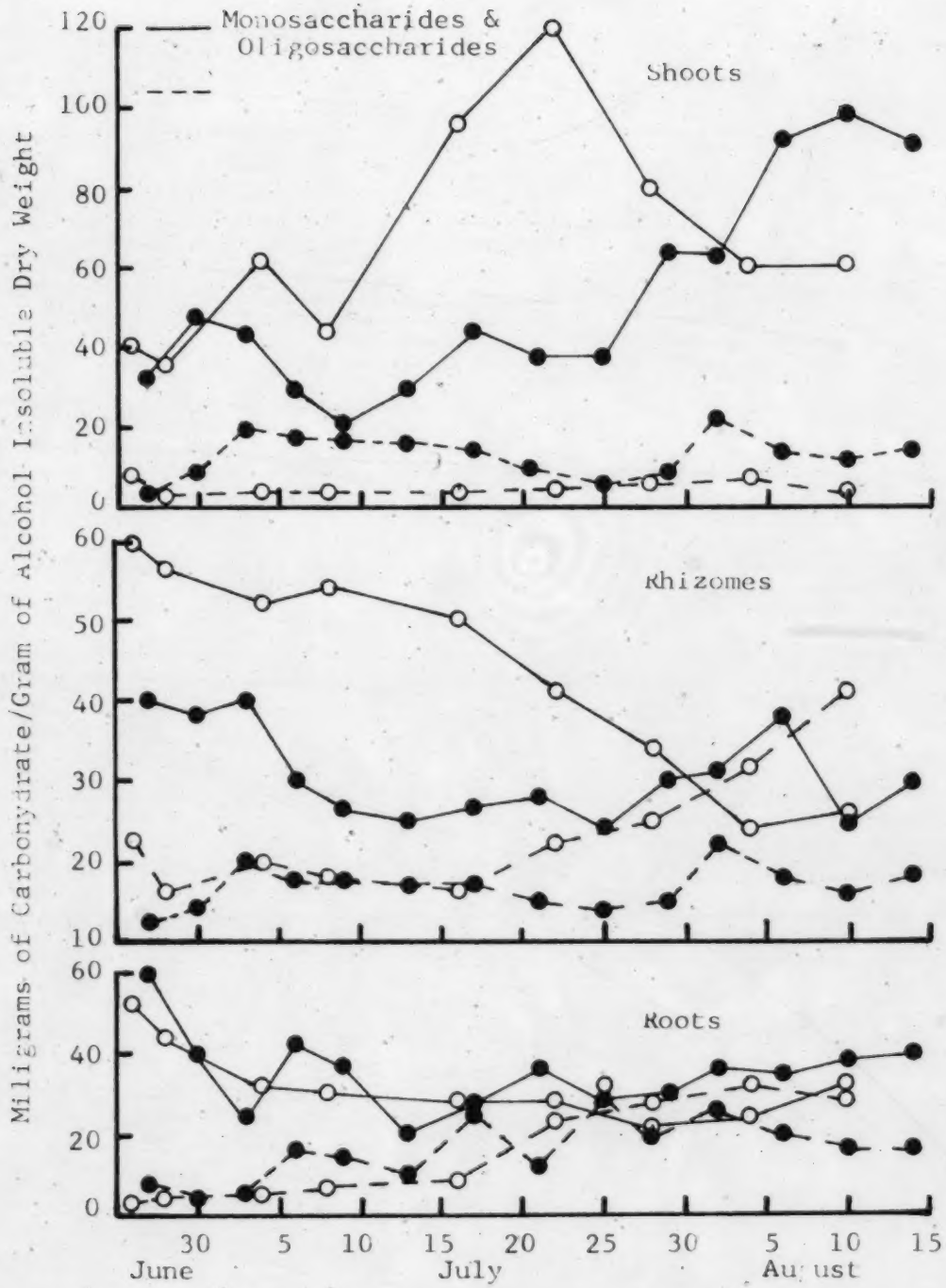

Figure 46. Seasonal changes in Carex membranacea (closed) and C. stans (open) shoot, rhizome, and root carbohydrate content.

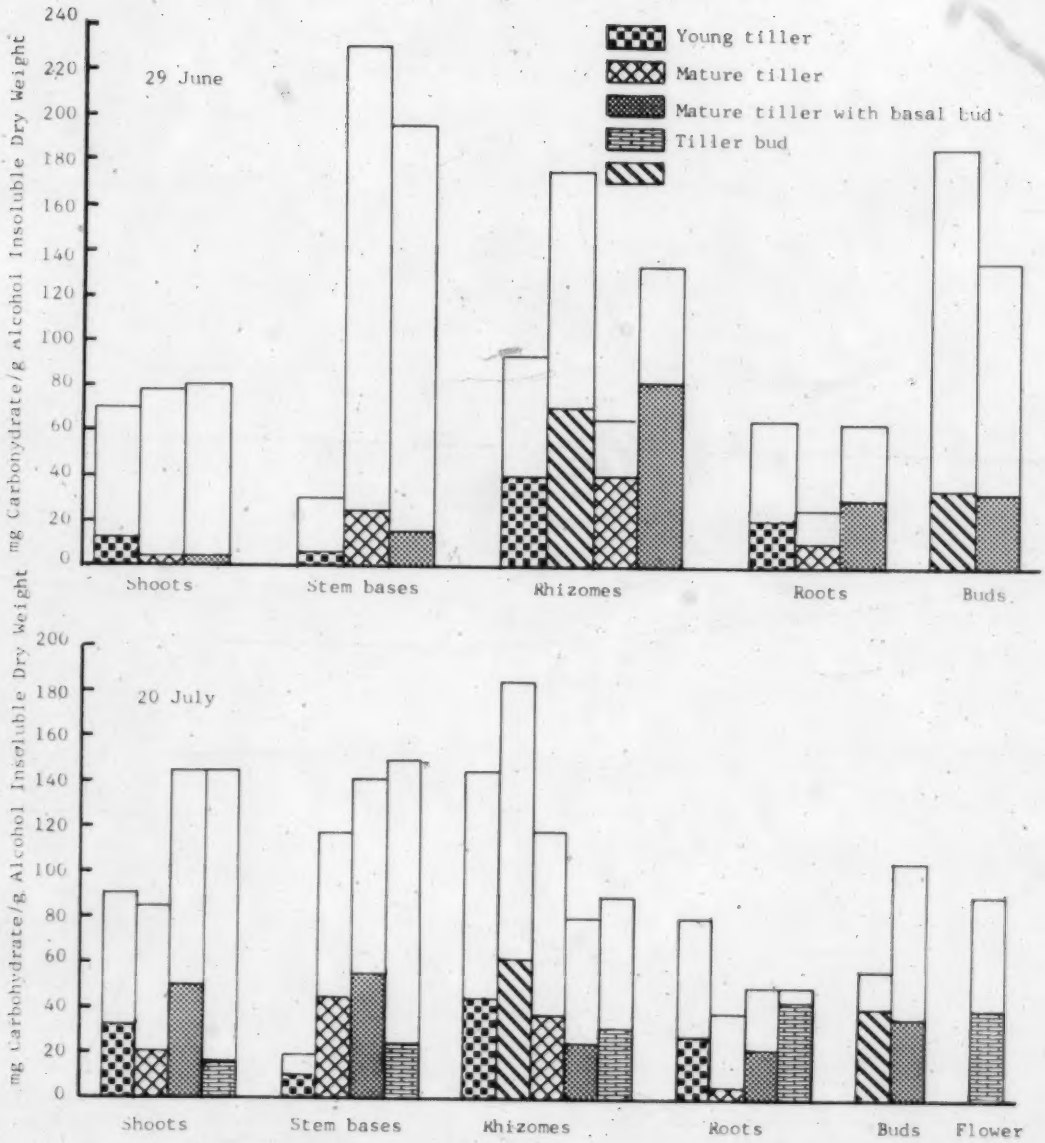

Figure 47. Seasonal changes in the monosaccharide plus oligosaccharide (open) and polysaccharide (blocked) content of Carex stans tissue in phenologically distinctive tillers at the hummocky intensive study (site 1) meadow 1972.

In tillers with a bud, the bud carbohydrate levels were slightly higher than those in the rhizome. At the peak of the season, sexually and asexually reproductive sedge shoots had higher (75%) carbohydrate content than did shoots of non-reproductive tillers. Stem base carbohydrate levels were similarily higher (50%) but the reverse was found in a comparison of rhizome (70%) and root (20%) carbohydrate concentrations. Tiller flower and bud tissues possessed similar carbohydrate content. Young sedge tillers had a higher (50%) carbohydrate content, than did mature tillers, in their belowground structures but lower concentrations in their shoots (25%) and stem bases (85%).

Discussion

The early season depletion of belowground carbohydrates in sedge roots and rhizomes coincided with intensive post-snowmelt shoot growth. Rhizomes, by virtue of their higher (25 - 150%) carbohydrate content, appeared to be more important reserve sinks than were roots. Their location at the moss/soil interface would provide them an early spring thaw and allow them to actively translocate carbohydrates to the shoots well before the rooting zone became thawed. Root carbohydrate reserves might therefore play a more important role in shoot growth later on in the growing season. Replenishment of the carbohydrate content of these belowground structures did not occur until after peak seasonal aboveground growth had been attained.

Cook et al. (1962) found replenishment of depleted belowground reserves, in temperate monocots, to occur when a critical carbohydrate depletion threshold was reached. This critical level was on the order of 20 - 30% of the maximum carbohydrate reserve. The comparable critical level calculated for Carex membranacea and C. stans was on the order of 50 - 60% of the maximum carbohydrate reserve. Maintenance of such a high critical level would appear to be an added measure of protection against serious reserve depletions which might be difficult to replenish during such a short growing season. Sedges overwintering with lower root and rhizome carbohydrate levels might also develop a lower degree of frost hardiness and experience a reduced ability to initiate and maintain an active level of early season shoot growth.

Lower temperatures, as found in the latter part of the meadow growing season, appear to act as a stimulus for belowground carbohydrate accumulation (Spomer and Salisbury 1958, Fonda and Bliss 1966). A significant reduction in shoot growth at this time must also play a role in initiating translocation of carbohydrates into belowground structures. The overall meadow sedge carbohydrate cycle is similar in its seasonal dynamics to the one found in raised beach plants (Svoboda 1976); to the one in low arctic monocots (McCown and Tieszen 1972); and that of alpine sedges (Fonda and Bliss 1966).

Aboveground sedge shoot growth and translocation of

belowground carbohydrates, as evidenced by their seasonal depletion, to these tissue appeared to be interrelated. In both Carex membranacea and C. stans, belowground carbohydrate depletions became substantially reduced when 75 - 80% of the seasonal shoot growth was complete. Billings and Mooney (1968) indicated that such translocation in arctic plants occurred until 80% of shoot growth was complete. Jenkin (1972) found that in sub-antarctic plants translocation continued on until 75 - 90% of shoot growth was completed.

The seasonal growth of root and rhizome tissue was considered to have its main development in the latter part of the growing season. In many plants aboveground tissue growth has a priority over belowground growth (Wardlaw 1968). Late season belowground tissue increment would benefit not only from the decrease in aboveground demands for carbohydrates but also from the more pronounced translocation of carbohydrates into these belowground sinks.

Average sedge tiller total carbohydrate levels rose from an early season value of 17% of the total tiller weight to late season levels of 24%. It was found that tiller carbohydrate reserves increased by 20% the year after an earlier and milder growing season. Such an increase might explain the higher sedge flowering rates which also found following such an early and mild season. The substantial (40 - 140%) increase in the carbohydrate content of wet meadow sedges, as compared to those in the hummocky meadow, was considered to be a response to the colder soil

temperature regimes found in these meadows. These higher carbohydrate levels were also reflected in higher sedge flowering rates in the wet meadow. It would appear that carbohydrate content and flowering, in meadow plants, were closely associated with one another.

The 17 - 24% carbohydrate weight content of sedge tillers is almost half the carbohydrate content (30 - 40%) reported (McCown and Tieszen 1972) for low arctic monocts but is similar to the 18 - 20% found in alpine sedges (Fonda and Bliss 1966). Carbohydrate levels of raised beach plants were slightly less than 10% (Svoboda 1974). Warren Wilson (1966) indicated that the average carbohydrate content of arctic species was on the order of 15 - 30%. It would appear that a dependence on carbohydrate reserves was of greater importance to arctic meadow plants than it was to raised beach species. In large part this would be associated with a growth strategy which concentrated its biomass belowground (meadow species) rather than aboveground (raised beach species). High plant carbohydrate requirements for growth have been found necessary in order to offset low levels of nitrogen availability (Graber 1931, Black 1968). The low nitrogen levels in the lowland meadows (Babb and Whitfield 1976) may well be an added stimulus for causing meadow plants to develop substantial carbohydrate reserves.

Overall seasonal sugar:starch ratios were lower in aboveground tissue than they were in belowground tissue. Starch content of overwintering sedge tissue was less than

15% of the total carbohydrate content. Higher tissue sugar concentrations were found associated with colder temperatures and were considered to be involved in frost hardiness development. Substantial starch hydrolysis was found to occur as temperatures dropped in the latter part of the growing season. Earlier on in the season, the warmer temperatures appeared to favor sugar to starch conversion. The higher sugar concentrations in the shoot tissue were interpreted as providing a more mobile carbohydrate resource for growth. These carbohydrates would also be more easily translocated belowground at the end of the season. Higher starch concentrations in belowground tissue were considered to provide these tissue with a higher energy source for their growth later on in the season.

The high (85% of total reserves) tissue carbohydrate content contributed by sugars, in overwintering sedges, was associated with their involvement in developing frost hardiness. Increased cellular sugar levels are known to increase a cell's osmotic pressure and provide protection against protein denaturation (Levitt 1956, Levitt 1960). This would occur as a result of the reduction in the freezing point of the cell sap as well as through a reduction in formation of intra-cellular ice crystals. Starch granules, on the other hand, would have served as nuclei for such cellular ice crystal formation and impeded frost-hardiness. Parker (1963) found that high tissue sugar levels at the beginning and end of the growing season were characteristic

of plants which were capable of developing frost hardiness.

The high (98%) oligosaccharide composition of the sedge carbohydrates appeared to be characteristic of plants with carbohydrate cycles. Similar concentrations were reported for raised beach species (Svoboda 1972), alpine (Fonda and Bliss 1966), and temperate (Miller 1924) species. Such high oligosacchardie levels would be expected since the bulk of the carbohydrates occur as sucrose.

Aboveground carbohydrate concentrations in mature sedge tillers were 30 - 665% higher than those in young tillers. Significant aboveground carbohydrate levels were found in all tillers only after the full leaf compliment had been devloped. Belowground carbohydrate levels of the young tillers were 80 - 100% higher than those in mature tillers. Rhizome carbohydrates were 50 - 70% higher than those in roots and appeared to be the main energy resource for the early season shoot growth in the young tillers. Russell (1940, 1948) found similar high belowground carbohydrate reserves in other arctic species which were undergoing active shoot growth. In temperate monocots, high rhizome carbohydrate levels are considered to act as a stimulus for tiller and bud initiation (Jameson 1963).

Mature tillers which were not reproductive, were found to possess the lowest carbohydrate concentrations in both aboveground and belowground structures. Rootless young tillers were found to have high carbohydrate levels in their rhizomes. This might be interpreted on the basis of

carbohydrate translocation between these tillers; the productive mature tillers making their carbohydrates available to the dependent young tillers. Low arctic Carex aquatilis tillers were found to produce roots by the second season and to be dependent on mature tillers until that time (Shaver and Billings 1975). Similarily, the lower rhizome and root carbohydrate levels in mature tillers with developing tiller buds would indicate a similar carbohydrate dependence. In temperate monocots, Williams (1964) found that buds and tillers readily imported carbohydrates from more mature plants. Such a carbohydrate relationship between sedge tillers at different phenological stages of development would insure greater tiller survival through maximum efficiency in utilization of carbohydrate reserves.

Reproductive sedge tillers were found to increase their aboveground carbohydrate reserves at the expense of belowground tissue. At peak season, belowground carbohydrates in these tillers were 70% lower in rhizomes and 20% lower in roots than were those of comparable non-reproductive tillers. Carbohydrate levels were similar in both flowering and vegetative bud tissues. Considering that meadow sedge flowering is almost totally unsuccessful, carbohydrate expenditures in sexual reproduction appear highly impractical. Flowering rates are low and the majority of reproduction is by vegetative means. Lewis et al. (1972) found that failure to set seed in Phleum alpinum resulted in the tiller's death but also resulted in the initiation of another tiller off

the dying tiller. Although this relationship was not examined in the sedges, it was observed that the majority of tillers on belowground systems occurred in distinctive clumps. This could be interpreted that the same process occurs in high arctic sedges and that it insures that the tillers energy and nutrient resources are used to maintain the tillering system.

CHEMICAL COMPOSITION

Energy (caloric) content of arctic vascular plants is higher than that of temperate and tropical species (Golley 1961, Bliss 1962b). High tissue energy levels and low seasonal variability of this component are important adaptive features of arctic meadow plants.

Low soil nutrient availability, especially of nitrogen, has been considered (Russell 1940, Porsild 1951) a major limitation in arctic plant growth. Arctic plants may, however, be adapted to growing under low soil nitrogen availability (Savile 1972). Although the majority of the meadow nutrient pool was frozen in the permafrost, meadow plant growth appeared to indicate efficient utilization of the available soil nutrients.

Seasonal chemical content of low arctic meadow plants has been widely reported from a number of areas (Kovakina 1958, Pieper 1963, Wielgolaski 1971b, Scotter 1972, Haag 1974). Soil nutrient content of low arctic meadows has also been studied (Gersper 1972, Haag 1974). Equivalent high arctic

data have been presented by Bunting and Hathout (1971) and Walker and Peters (1976)

Methods

Energy Content

In 1970, energy content determinations were made on tissues of the major meadow species (Carex stans, Carex membranacea, C. misandra, Eriophorum angustifolium, Arctagrostis latifolia, Salix arctica, Polygonum viviparum, Equisetum arvense, and Pedicularis sudetica) at the hummocky intensive study (site 1) meadow. Analyses were made on plant materials collected for production studies (n=5 harvests). Soil organic matter and litter were also analysed from each harvest. In 1971, energy content was only determined for live and dead Carex stans shoots collected in early, peak, and late season.

All harvested tillers were sorted into live shoot, dead shoot, live stem base, dead stem base, total root, rhizome, and dead plant components. The dried (85° C for 24 hr) plant material was ground on a Wiley Mill to pass through a 20 mm mesh and duplicate samples analysed for caloric content (±1% standard error) on an Automatic 1200 Adiabatic Oxygen Bomb Calorimeter (Parr Instrument Co., Ltd.). Ash content was calculated from the weight of post-combustion residues.

Chemical Content

Only Carex stans, the dominant meadow species, provided sufficient material for chemical analyses. These analyses, made on 1970 and 1971 tillers harvested for production studies,

were carried out by the Soil and Feed Testing Laboratory of the Alberta Department of Agriculture, Edmonton. Analytical methods used were those of the Association of Official Agricultural Chemists (1955). Tissue protein content was equal to tissue nitrogen content X6.25. All values are expressed as a percentage of total dry weight.

Results

Energy Content

Intersite and seasonal variation in meadow plant energy content was less than 2%. Woody plants developed the highest energy content and pteridophytes the lowest (Table 28). The energy content of live and dead monocot and pteridophyte tissue was similar but the former tissue had slightly higher (2.5%) energy content in forbs and woody plants. Totally dead plants were of a slightly higher (4%) caloric content than were totally live plants. Energy content of individual meadow species was reported in an earlier paper (Muc 1972).

The seasonal energy content of the meadow soil organic matter averaged 4837 cal/g and was only slightly (3.5%) higher in the upper 10 cm of the profile (Muc 1972). Meadow litter had an average energy value of 4808 cal/g and it ranged from an early season high of 4963 cal/g to a low of 4673 cal/g by the end of the season.

Ash content of the meadow plants was low and ranged from 1.9 - 6.6% in living plant material to 3.6 - 6.4% in dead plant material. Woody plant tissue had the lowest ash content and pteridophyte material the highest. Extremely high ash

Table 28. Average seasonal non-ash free energy (cal/g dry wt) and ash (%) content of aboveground and belowground components of major meadow plant groups (hummocky intensive study meadow, site 1) 1970.

Plant Component	Plant Group			
	Monocots	Forbs	Woody Plants	Pteridophytes
Live shoots	4785	4965	5100	4586
(ash)	4.0	5.2	3.8	6.6
Dead shoots	4777	4743	5002	4507
(ash)	4.5	3.6	3.9	6.4
Stems	4789	____	5106	____
(ash)	4.1	____	1.9	____
Roots	4670	4703	5106	____
(ash)	3.3	4.4	4.0	
Rhizomes	4650	____	____	____
(ash)	2.7	____	____	____
Total live plant	4734	4804	5071	4547
(ash)	3.7	4.4	3.4	6.5
Total dead plant	4901	____	5282	____
(ash)	5.6	____	3.7	____

levels of 14 - 31% were found in the soil organic matter.

Chemical Content

Data on the fall (August - October, 1971) chemical content of aboveground meadow plant material were based on materials collected by Ben Hubert (Table 29). The plants were not sorted into live and dead components and the latter material made up over 85% of the total plant weight. Forbs had the highest nitrogen, calcium, and phosphorus content. Woody plant and forb lignin content was 195 and 85%, respectively, higher than in monocots. Woody plants possessed the highest lipid (fat) levels. Fall nitrogen, phosphorus, and lipid content of meadow plants showed an overall gradual decrease. Tissue lignin content of woody plants and forbs increased over the same period. Calcium levels showed no consistancy in their development and appeared to increase in forbs and decrease in monocots.

Annual variation in chemical content of Carex stans tissue was on the order of 20% and seasonal variation was on the order of 15% (Table 30). Chemical content of belowground material peaked by early July and not until late July in aboveground tissue. Mid-August decrease in the chemical content of aboveground tissue was reflected in an increase of these chemicals in belowground tissue. This was the reverse of the situation found in the early part of the season.

Chemical levels (excluding calcium) in aboveground Carex stans tissue were on the average 120% higher than in below-

Table 29. Chemical composition (%) of total (live and dead) aboveground tissues of the three major meadow plant groups collected from various lowland hummocky meadows 1971 (Data provided by B. Hubert).

Plant Group	Month	Chemical Composition (%) Nitrogen	Calcium	Phosphorus	Lipid	Lignin
Forbs	August	2.99	0.58	0.37	1.5	11.1
	September	2.94	0.55	0.30	1.5	12.7
	October	2.00	0.88	0.20	1.9	13.1
	Mean	2.64	0.67	0.29	1.6	12.3
Woody Plants	August	1.46	0.86	0.15	2.2	14.6
	September	1.42	0.96	0.12	1.8	17.1
	October	1.22	0.70	0.09	...	26.9
	Mean	1.36	0.84	0.12	2.0	19.5
Monocots	August	1.66	0.89	0.12	2.5	7.4
	September	1.30	0.86	0.12	1.5	7.5
	October	1.14	0.47	0.09	1.0	4.8
	Mean	1.37	0.74	0.11	1.7	6.6

Table 30. Chemical composition (%) of aboveground and belowground *Carex stans* tissues and soil organic matter (hummocky intensive study (site 1) meadow) 1970, 1971.

Tissue	Date	Nitrogen	Calcium	Phosphorus	Potassium
ABOVEGROUND	1970				
Live shoots	1-7	2.78	0.17	0.28	1.66
	22-7	3.52	0.28	0.28	1.90
	17-8	3.44	0.27	0.29	1.86
	1971				
	8-6	2.69	0.17	0.25	———
	2-8	3.34	0.31	0.25	———
	5-9	2.73	0.17	0.29	———
	1970				
Dead shoots	1-7	1.47	0.79	0.10	0.27
	22-7	2.05	0.99	0.15	0.53
	17-8	1.70	0.87	0.10	0.34
	1971				
	8-6	1.41	0.73	0.07	———
	2-8	1.52	0.99	0.09	———
	5-9	1.36	0.86	0.08	———
	1970				
Live stem bases	1-7	2.77	0.23	0.34	1.78
	22-7	3.34	0.25	0.44	2.39
	17-8	2.48	0.20	0.36	1.70
	1970				
Dead stem bases	1-7	1.33	0.76	0.07	0.13
	22-7	1.42	0.69	0.10	0.24
	17-8	1.25	0.70	0.10	0.23
BELOWGROUND					
	1970				
Roots	1-7	1.34	0.67	0.12	0.33
	22-7	1.23	0.37	0.08	0.33
	17-8	1.30	0.32	0.21	0.42
	1970				
Rhizomes	1-7	1.46	0.42	0.16	0.35
	22-7	1.22	0.35	0.12	0.43
	17-8	1.28	0.23	0.17	0.55
	1970				
Dead plants	1-7	1.62	1.11	0.10	0.13
	22-7	1.47	0.78	0.10	0.17
	17-8	1.33	0.63	0.13	0.16
	1970				
Soil organic matter	1-7	2.61	2.06	0.14	0.10
	22-7	2.58	1.90	0.15	0.15
	17-8	2.62	1.74	0.13	0.12

ground tissue. Chemical levels in aboveground live shoot and stem bases were very similar as were those in dead shoot and stem base tissue. Live aboveground plant material did develop 95 - 115% higher nitrogen, 200 - 320% higher phosphorus, and 375 - 880% higher potassium levels over those developed in comparable dead tissue. Little seasonal variation, except in calcium, was found in the chemical content of soil organic matter (Table 30). Soil organic matter content appeared to lose its calcium over the season.

Discussion

Energy Content

The relatively stable energy levels in meadow plants suggested seasonal stability in the plant component of the meadow energy budget. The slight seasonal energy changes that were found could be attributed to changes in tissue hemicellulose levels (Roshchevskaia and Schvetsova 1970), phenological changes, carbohydrate translocation, and tissue lipid changes. Seasonal energy content of low arctic (Tieszen 1970) and alpine (Bliss 1962b) meadow plants was found to vary less than 5%.

The higher energy content of the meadow woody plants was proportional to their higher lignin and lipid content. The lower energy levels found in belowground plant material were due to the lower lignin and lipid, as well as higher carbohydrate, content of these tissues. Similar aboveground and belowground energy differences have been found in alpine meadow plants (Hadley and Bliss 1964). The apparent increase

in plant energy content along a latitudinal and decreasing temperature gradient may be explained on the basis of increasing tissue lipid levels (Bliss 1962b, Tieszen 1970).

The small (6%) seasonal change in energy content of meadow litter was considered to result from leaching and decomposition. The slight (< 4%) increase in the energy content of organic matter in the lower soil profile may have developed through the process, reported by Malone and Swartout (1969), of tissue carbon concentration as a result of chemical leaching. On a community basis, dead meadow plant materials constituted a large energy sink. The concentration of over 95% of the meadow biomass belowground insured maximum energy retention within the meadow community. Such energy considerations were undoubtedly prominent in the successful development and productiveness of these lowland communities.

The 2 - 6% ash content of lowalnd meadow plants was twice as high as that of alpine meadow species (Bliss 1962b) but similar to that of Eurasian arctic meadow plants (Chepurko 1972). The higher ash content of the lowland meadow plants was developed from their higher tissue mineral content. The high ash content in pteridophyte tissues were derived from the high silica concentrations (Wilson and Loomis 1967) in their fiber and epidermal cells. High ash levels in the soil organic matter were a result of extracellular mineral contamination by the soil mineral fraction.

Chemical Content

The average fall lipid content (1.6 - 2.0%) of meadow plants was similar to that of alpine meadow species (Bliss 1962b) but considerably lower than the lipid content of Barrow (McCown and Tieszen 1972) monocots. Low tissue lipid levels appear to be characteristic of asexually reproductive plants (McNair 1945). Beach ridge cushion plants had tissue lipd levels of 2.5 - 9.7% (Svoboda 1974). Monocot and forb lipid content decreased in the late fall, a pattern similar to that found in low arctic species (Scotter 1972). This decrease in lipid content may have been associated with metabolic utilization necessitated by the low fall temperatures. McCown and Tieszen (1972) found that in low arctic meadow monocots, high spring polysaccharide reserves were used to synthesize a fatty acid pool for early season growth metabolism. Lipids, although low in content, appear to be important in arctic plant metabolism and may be most significant in early and late season metabolism.

Fall nitrogen and phosphorus levels in meadow forbs were 95 - 165% higher than those of monocot and woody plants. The similarity in chemical content of monocot and woody plant tissues, coupled with their larger belowground storage sinks, suggested a greater translocation of their aboveground chemicals into these belowground tissues.

Overall meadow plant chemical levels were similar to those of low arctic meadows (Pieper 1963, Haag 1974). The pronounced fall decrease in tissue chemical content observed

in the lowland meadow plants appears to be common in arctic meadow species (Pieper 1963, Scotter 1972). Leaching and decomposition (Widden 1976) would account for a portion of this change and the remaining portion may result from a translocation of aboveground minerals into belowground tissue.

Live aboveground Carex stans tissues had 95 - 115% more nitrogen than was found in aboveground dead tissues. This indicated rapid nitrogen mineralization in dead aboveground tissues. The low tissue nitrogen levels in belowground structures would result in a decrease in the decomposition rates of these tissue (Alexander 1967). Sedge phosphorus levels were less variable than those of nitrogen, a condition common in other low arctic (Haag 1974) and Norwegian alpine (Wielgolaski and Kjelvik 1973) meadow plants. The more pronounced seasonal dynamics of tissue nitrogen might be interpretted as an indication that this nutrient is of considerable importance to meadow plant growth. Low soil levels of this nutrient would be limiting to meadow plant growth.

Lowland sedges had similar nitrogen, phosphorus, and potassium concentrations to those found in Norwegian alpine (Wielgolaski 1971b) sedges. Calcium content of the latter sedges was 25 - 55% higher but may have reflected more alkaline soil conditions.

Nitrogen, phosphorus, and potassium were readily recycled, through leaching and decomposition, in the meadow

nutrient pool. Calcium,-a highly immobile element, was not readily recycled and became a larger component of dead plant tissue as the more mobile elements were lost. Peak concentrations in tissue chemical content occurred prior to peak biomass development. Post biomass peak tissue chemical levels dropped by 10% a condition attributed to reduced plant growth (demand?) and the developing phenological changes which might influence redistribution of tissue chemicals. Movement of tissue chemicals between aboveground and belowground structures was apparent from the early and late season chemical data. High chemical concentrations in belowground tissues at the beginning of the season corresponded to lower levels in aboveground tissues. The reverse condition was found at the end of the season. This pattern of nutrient utilization by meadow plants would help to offset low soil nutrient availability.

The nitrogen content of soil organic matter was found to be 75% higher than that of totally dead plants. Meadow plant roots, growing adjacent to this nitrogen pool, had the level of available nitrogen regulated by the slow (Widden 1976) decomposition rates occurring in this component. Organic matter content was also 130% higher in its calcium content but had 25% less potassium than was found in totally dead plants. Phosphorus release through decomposition was lower than that of nitrogen (Haag 1974) and resulted in a 25% increase in the phosphorus content of soil organic matter over that found in totally dead plants.

Hummocky sedge-moss meadows had the highest levels of available soil nutrients (N,P,K) and wet sedge-moss meadows the lowest levels (Walker and Peters 1976). Maximum available nutrient concentrations were found in the upper 5 cm of the soil profile. This reflected the warmer soil temperatures, lower soil moisture, and higher microbial populations associated with these shallow depths. Available nutrient levels dropped 25 - 100% at the lower soil depths. Effective nutrient uptake and recycling in the lowland meadows appeared to be at its maximum in the upper 5 - 10 cm of the soil profile. These factors were severely depressed at the lower soil depths by not only lower nutrient levels but also by a physiological limitation (Sørensen 1941, Haag 1974) to nutrient uptake created by the lower soil temperatures. Maximum belowground biomass concentration and increment was also associated with the upper soil profile.

SUMMARY

Sedge-moss meadows were not only the dominant Truelove Lowland plant community with respect to area cover (41%) but also in their capacity to maximize biomass, energy production, and nutrient flow. Lowland meadow development was closely associated with drainage impoundment a situation arising from raised beach formation. Radiocarbon datings of peat deposits near raised beaches of known age, indicated that meadow development began ca. 2500 - 3000 years later. At the present time the most intensive meadow formation was occurring in the most recently emerged portions (western coastline) of the lowland.

Temperature and nutrient limitations to plant growth, considered to be characteristic of the high arctic ecosystem, also operated in the meadow communities. Warmer air temperatures such as those developed in the field greenhouses and nutrient supplements (Babb 1972) to the meadow soils were found to produce a positive effect on plant growth and production. Low meadow soil temperatures offset the advantages to be gained from the high soil moisture levels. Addison (1976) found meadow Carex stans to experience water potential stresses (physiological drought?) as severe as those measured in Dryas integrifolia on the dry raised beaches.

The lowland meadows developed along an increasing soil moisture gradient. Frost-boil meadows with characteristic prominent and poorly vegetated mineral frost-boils, interspersed amongst areas of organic matter accumulation and

extensive plant cover, occupied a relatively 'dry' habitat. Wet meadows developed within flooded habitats and consequently had a more uniform environment which favored a lusher and more homogeneous plant cover. The hummocky meadows had a mesic type of habitat in which characteristic hummock and hollow microhabitats formed. These microhabitats had associated with them, a distinctive pattern of plant distribution and cover. The hummocks were heavily vegetated with forbs, woody plants and monocots while the hollows were vegetated, to a lower extent, almost singularly by monocots.

A total of 34 vascular species provided the overall meadow plant diversity. Carex stans was the characteristic lowland meadow species. Species diversity in lowland meadow stands ranged from 17 - 23 and vascular plant cover ranged from 54 - 91%. The most extensive vascular plant cover developed in the hummocky meadows and the lowest in the frost-boil meadows.

A deep (39 - 52 cm) snow cover provided meadow plants with an effective insulation against the rigors of a lengthy arctic winter. Spring melting of this cover provided the meadow community with the major portion of its soil moisture (Ryden 1976). Although growing season air temperatures averaged less than 10° C and soil temperatures averaged less than 5° C, Carex stans was still capable (Mayo et al. 1976) of active photosynthesis at such low temperature regimes. Meadow soil thaw was most pronounced in the early part of the growing season when incoming radiation levels were high.

Peak soil thaw (27 - 58 cm) in the lowland meadows occurred by early to mid-August. Seasonal variation in meadow soil thaw depth was less than 10 cm and the deepest thaw was found in the poorly vegetated, mineral frost-boil soils.

Sedge-moss meadow soils were either Gleysolic Turbic Cryosols, Gleysolic Static Cryosols, or Fibric Organo Cryosols. The gleysolic soils were characteristically deeper thawing, colder, and potentially active (cryoturbation). The organic soils presented a more optimal growth habitat and this was evidenced in a greater plant cover and larger belowground biomasses. Frost-boils were the poorest habitat for vascular plants and developed plant covers of 10 - 15%. Hummocks were better drained, better aerated and warmer than the corresponding hollow habitats. This resulted in their developing a higher (ca. 50%) plant cover.

The average potential growing season in the lowland meadows was 50 days in duration but net positive leaf length increment (=actual growing season?) was only found over 20 days in forbs and woody plants and over 40 days in monocots. Seasonal meadow plant growth dynamics varied little and growth was found to begin immediately after snowmelt (late-June to early-July) and to terminate (early to mid-August) two to three weeks before the onset of permanent inclement weather. Growth was closeley associated with incoming radiation and temperature regimes.

The majority (65 - 70%) of the sedge tillers were clumped in their distribution along the belowground tiller

system. This was interpreted as showing that new sedge tillers were being developed off (by?) dying tillers. A reproductive strategy of this type would insure greater tillering success. The established root and rhizome systems of the dying tiller would sustain the developing tillers until they had developed their own belowground systems. Monoct leaves were found to remain alive for two seasons and to remain attatched for another three seasons. Tiller life spans were estimated to be on the order of 5 - 7 years. Roots remained alive 1 - 3 years longer than their aboveground shoots and functioned in the formation of new tiller establishment.

Vegetative reproduction was the most extensive and successful method of reproduction in the meadow plants. Flowering occurred in less than 10% of the meadow population but successful seed set was never observed in the lowland meadows. The short growing season did not make sexual reproduction practical but its occurrence would maintain a potential for genetic variability if it should ever be needed. Flowering rates in any given year reflected the previous year's climatic conditions. Higher flowering rates were found the year after an earlier and milder growing season even if the season itself was late and cool. The reverse situation developed after a late and cool growing season. Higher (7° C) greenhouse air temperatures caused sedge flowering rates to double over those in control conditions. This suggested that temperature was a vital factor in meadow

flowering.

Meadow monocots and forbs overwintered with an average of 6 g/m^2 of green (photosynthetic) tissue. This green component provided these plants with the basis for initiating rapid early season growth. Peak total standing crops in the lowland meadows increased along an increasing moisture gradient. The lowest biomass levels (821 g/m^2) were found in the 'dry' frost-boil meadow and the highest (2316 g/m^2) in the mesic hummocky meadow. Stagnant waters in the flooded wet meadow depressed the vascular biomass to only 1570 g/m^2.

Of the total average meadow aboveground biomass which ranged from 170 - 282 g/m^2, monocots contributed 85 - 95%, woody plants 0 - 10%, and forbs 5% of the total biomass. In the aboveground component, dead plant material was 55 - 115% higher in its content than live material but in the belowground component it was slightly (5%) lower. Total belowground standing crops averaged 651 - 2034 g/m^2 and represented 80 - 88% of the total meadow vascular plant biomass. Meadow roots were concentrated (80%) in the upper 20 cm of the soil profile. This portion of the soil profile represented the most optimal growth conditions.

Of the net aboveground production in the lowland meadows, 70 - 95% was by monocots, 0 -25% by woody plants, and 0 - 5% by forbs. Average production ranged from a low of 28 g/m^2 in the frost-boil meadow to a high of 45 g/m^2 in the wet meadow. This reflected an increasing development of the.

optimal habitat for Carex stans the dominant meadow species. Corresponding growing season productivity ranged from 0.54 - 0.88 g/m^2/day. Belowground production was 200 - 250% higher than the aboveground meadow production and was considered to have its maximum development in the latter part of the growing season. Belowground production ranged from a low of 59 g/m^2 in the frost-boil meadow to a high of 128 g/m^2 in the wet meadow. This represented an average total biomass increment of 5%. Monocots contributed approximately 95% of the belowground production and of this total 5% was from rhizome increment. Growing season meadow productivity ranged from 1.16 - 2.51 g/m^2/day. The overall total vascular production of the lowland meadows ranged from 87 g/m^2 in the frost-boil meadow to 174 g/m^2 in the wet meadow. This represented a total productivity of 1.70 and 3.39 g/m^2/day, respectively.

Meadow litter standing crops had peak development (6 - 12 g/m^2 average) immediately after snowmelt. Litter constituted approximately 20% of the total shoot biomass and indicated a shoot - litter turnover rate of 5 years. Fibric Organo Cryosols developed soil organic content levels 30 - 175% higher than those found in the Gleysolic Cryosols. Associated with these former soils were lower soil densities and higher soil nutrient levels which helped to create a more optimal rooting environment. Root biomass was consequently 110 - 210% higher in these soils.

The meadow plant canopy was less than 10 cm in height

and developed only two distinctive strata. The lower stratum was composed of forb and woody plant foliage and the upper stratum of monocot foliage. The shortness of the meadow growing caused a relatively parallel development and peaking of community chlorophyll content, photosynthetic leaf area, and green shoot biomass. Peak season meadow community chlorophyll content ranged from a low of 162 mg/m^2 in the frost boil meadow to a high of 283 mg/m^2 in the hummocky meadow. Corresponding leaf area indices of community photosynthetic material were 0.31 and 0.63, respectively.

Sedge tiller carbohydrate levels ranged from 17 -24% of the total tiller weight and were found to increase by 20% after an earlier and warmer growing season. Early season carbohydrate reserves were concentrated primarily in the rhizomes but aboveground growth was supported by carbohydrates from both rhizomes and roots. Depletion of these belowground reserves continued until 75 - 80% of the aboveground growth had been produced and it was not until after this period (late season) that the belowground reserves were rebuilt by translocation of aboveground carbohydrates. Overwintering sedge tillers maintained the bulk (90%) of their carbohydrates as sugars. During the course of the growing season 10 - 60% of the tiller carbohydrates were in the form of high energy starches. Oligosaccharides were the dominant sugars. Carbohydrates were not only important in initiating rapid shoot growth immediately after snowmelt but they were also crucial to the development of frost-hardiness.

Seasonal energy content of the meadow plants varied by less than 2% and the non-ash free caloric content was highest (5175 cal/g average) in the woody plants and lowest (4815 cal/g average) in the monocots. The higher caloric content of the woody plants was proportional to their higher lignin and lipid levels. The leaching and decomposition incurred in dead tissue resulted in their caloric content dropping by 200 cal/g. Tissue ash content of the meadow species was less than 6% and high ash content was associated with high tissue mineral concentration such as that found in forbs.

Forbs maintained the highest tissue concentrations of nitrogen and phosphorus while woody plants had the highest calcium, lignin, and lipid levels. All of these constituents were in lowest concentrations within the monocot tissues. Sedge tiller tissues had low ($< 3.5\%$) levels of all the chemicals tested for. Tissue nitrogen content was 170 - 960% higher than that of potassium, phosphorus, or calcium. Peak tissue chemical levels developed prior to similar peaks in the plant biomass. Annual variation in sedge chemical content was on the order of 15% and was 20% over the course of the growing season. Aboveground live sedge tissues had a 120% higher chemical content than was found in dead and belowground tissues. Nitrogen, phosphorus, and potassium were highly mobile tissue chemicals and were readily lost from dead tissue. Calcium was highly immobile and increased in its proportional tissue weight value as these highly mobile elements were being recycled.

Soil moisture conditions were considered to be the single most important meadow environmental factor and regulated both community floristics and vascular plant production. This condition showed its maximum development in the flooded wet sedge-moss meadow habitats where the maintenance of a low species diversity allowed for the development of the highest meadow production. The highest meadow biomass content was found in the species diverse hummocky meadows but their production was lower because of this diversity. This developement between meadow species diversity and production is comparable to that proposed by Marglef (1969) for communities in general.

The successfulness of the lowland sedge-moss meadows was attributed to their efficient and conservative resource utilization. A schematic representation of what are considered to be the major energy and nutrient pathways and compartments in the sedge-moss meadow ecosystem are shown in Figure 48. Only 1 - 2% of the meadow biomass was considered to be potentially removed from the meadow system. The majority of the meadow energy and nutrient resources were retained within various compartments and recycled between these compartments. Efficiency in the utilization of resources in this manner allowed the meadow plants to partially counteract the effects of the short growing season and the low soil nutrient levels.

Aboveground, the majority of the vascular plant energy and biomass was concentrated in the dead plant compartment.

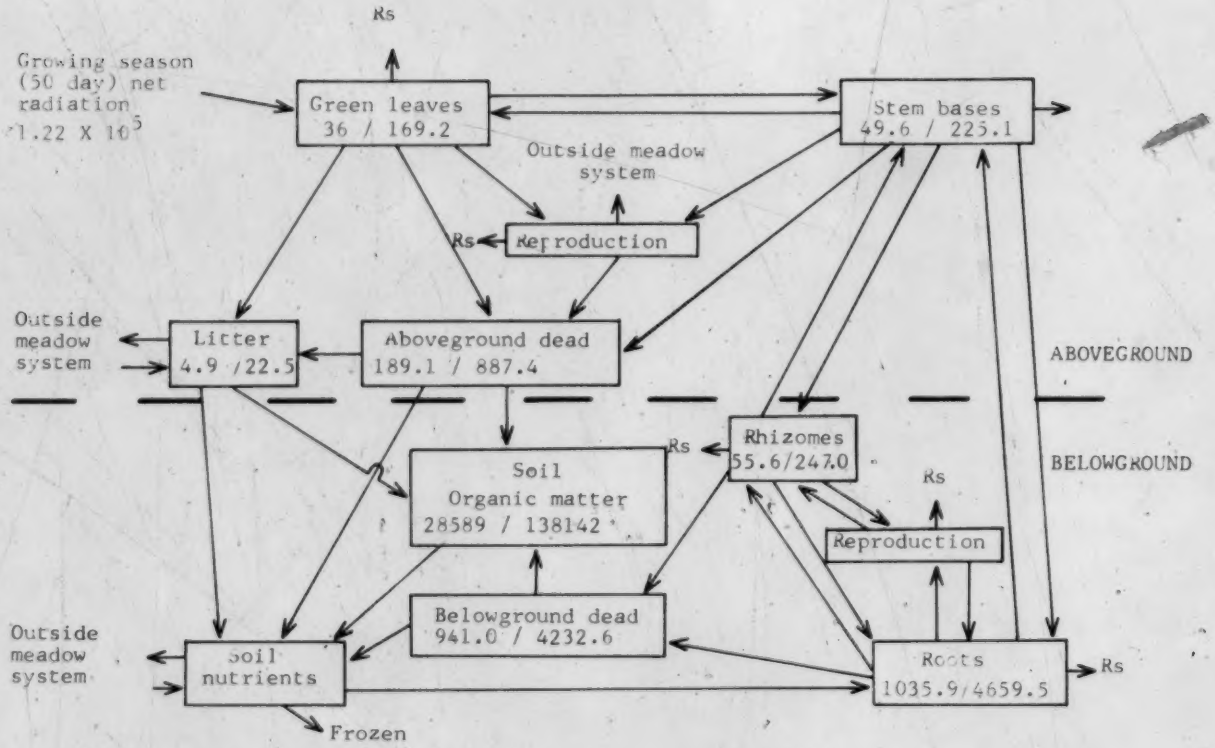

Figure 48. Energy and nutrient pathways of sedge-moss meadow vascular plant and soil components. Average peak season standing crop (g/m^2) / energy content ($Kcal/m^2$) presented for components sampled.

Of the live plant component, the majority of the reserves were retained in the non-green stem compartment which was concentrated in the moss layer. Belowground, the major concentration of energy and nutrients was maintained in the soil organic matter and live roots. The characteristic of concentrating biomass (=energy and nutrients) belowground was considered to be a prominent adaptive and survival feature of meadow plants. This growth strategy allowed them to survive and carry on growth under the adverse climatic conditions characteristic of the High Arctic.

Meadow plants also appeared to have their seasonal growth regulated, by as yet not understood, 'internal controls'. This would indicate that the environmental control of meadow plant growth was not as significant as it might have been expected. Internal control of growth would permit the plants to grow to the point where they accumulated sufficient reserves (carbohydrates) to insure them of successful growth the following season. This maximum growth level may have been 'set' to operate under the most rigorous (late, cool, and short) growing season conditions. A conservative growth pattern of this sort would limit the meadow plants from developing excessive growth in an earlier, warmer, and longer (more optimal?) growing season but this restriction would have been more than compensated for in their ability to maximize growth in a later, cooler, and shorter (less optimal?) growing season. Although each of the four growing seasons, during the duration of this study, was considerably different

from the others meadow growth and production were found to vary by only 10 - 20%.

The successful adaptation of the meadow plants to their environment played a prominent role in their extensive community development in the Truelove Lowland. Similarly, although sedge meadows are not a widespread high arctic community, they are its most important food base for the majority of avian and terrestrial fauna.

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